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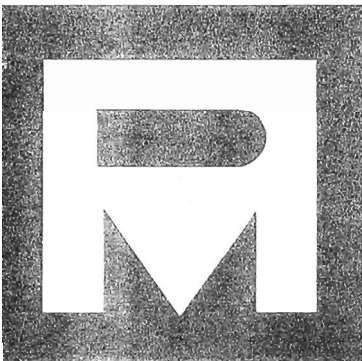
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PROSAUROPOD DINOSAURS (REPTILIA: SAURISCHIA) OF NORTH AMERICA

PETER MALCOLM GALTON

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ABSTRACT

The prosauropods from the Lower Jurassic Portland Formation of the Connecticut Valley are referred to two monospecific genera: the slender-footed *Anchisaurus polyzelus* (junior synomyns *A. colurus, Yaleosaurus colurus*) and the broad-footed *Ammosaurus major* (junior synonyms *Ammosaurus solus, Anchisaurus solus*); the material from Arizona is referred to *Ammosaurus* cf. *major*. The family Anchisauridae is restricted to three slender-footed genera (*Anchisaurus, Efraasia, Thecodontosaurus*); the remaining anchisaurids are broad-footed forms which are transferred to the family Plateosauridae along with *Ammosaurus*, a genus long regarded as an extremely primitive coelurosaur.

The replacement of prosauropods by ornithischians as the dominant "small- to medium-sized" (up to 10 m) terrestrial herbivores is attributed to the development in ornithischians of cheeks and self-sharpening teeth that dealt much more efficiently with resistant plant material than could the prosauropod dentition. The sauropodomorphs remained essentially quadrupedal, because they were herbivorous with the pubes anteroventrally directed as in most other reptiles.

1. INTRODUCTION

For about 15 million years until the end of the Triassic period some 200 million years ago the dominant large terrestrial herbivores were prosauropod dinosaurs, remains of which have been discovered in all continents except Antarctica. Particularly abundant and well-preserved remains have been described from Europe (Huene, 1907-08, 1926, 1932), South Africa (Broom, 1911; Haughton, 1924; Huene, 1932), South America (Bonaparte, 1972) and China (Young, 1951). To date only seven skeletal specimens of prosauropod dinosaurs, several of which are rather fragmentary, have been discovered in North America—from the Connecticut Valley and Arizona. However, despite the paucity of the material it is very important because the specimens from the Connecticut Valley, originally described in the latter half of the 1800s, occupy a central position in any systematic study of the Infraorder Prosauropoda (Suborder Sauropodomorpha, Order Saurischia). The specimens from the Connecticut Valley include the type species for three genera (*Anchisaurus, Ammosaurus, Yaleosaurus*). The type of *Anchisaurus (=Yaleosaurus) colurus* is the best-preserved skeleton of a small prosauropod of the family Anchisauridae. *Ammosaurus major* is important because Huene (1914a, 1932, 1956) considered the Ammosauridae to be the most primitive family of coelurosaurian dinosaurs (Suborder Theropoda, carnivorous, fast-running forms) rather than being prosauropods. Despite the importance of this material the descriptions to date are inadequate and much confusion exists concerning its systematic status. The purpose of this paper is to rectify that situation. A preliminary report on the North American prosauropods was published earlier (Galton, 1971a) as was a survey of the slender-footed prosauropods (Galton, 1973a). A full revision of the family Anchisauridae with a redescription of *Anchisaurus (Gyposaurus) capensis* (Broom, 1911) will be given elsewhere (Galton and Cluver, in press).

A historical survey of the discovery of the specimens with details of the localities is followed by an illustrated description of each specimen. The history of the systematic treatment of the material by various workers serves as an introduction to a critical discussion of the systematic status of the prosauropod taxa from the Connecticut Valley.

The following abbreviations of institutional names precede the specimen numbers referred to in the text and identify the repository of the specimens:

AM   Amherst College Museum, Amherst, Massachusetts
AMNH   American Museum of Natural History, New York
MNA   Museum of Northern Arizona, Flagstaff, Arizona
SMNS   Staatliches Museum für Naturkunde, Stuttgart, Germany
UCMP   University of California Museum of Paleontology, Berkeley, California
UT 1, 2   University of Tübingen, Germany; skeletons of *Plateosaurus* designated as Nos. 1 and 2 by Huene (1932)
YPM   Peabody Museum of Natural History, Yale University, New Haven, Connecticut

2. HISTORICAL SURVEY

All the prosauropod skeletal remains discovered in North America in the 1800s came from the Connecticut Valley. Lull (1915, 1953) gives a map showing the fossiliferous localities and quotes extensively from most of the descriptions published prior to 1912 as part of a detailed consideration of the complete fauna from the Upper Triassic of the Connecticut Valley. Shorter accounts are given by Lull (1912) and Colbert (1963, 1970). The bones of prosauropod dinosaurs came from the uppermost red sandstone bed of the Newark Series: either the Portland Arkose of Connecticut or the Longmeadow Sandstone of Massachusetts.

The earliest discovery was made in 1818 during blasting operations for a well in East Windsor, Connecticut. This find was reported by Smith (1820) who mentioned that the remains might be human, a possibility which was strongly disputed by Porter (*in* Hall, 1821) who noted the presence of tail bones, one of which was figured by Hitchcock (1841). This fragmentary material (YPM 2125) was identified as reptilian when described by Wyman (1855) and was subsequently referred to the prosauropod *Anchisaurus colurus* (see below) by Lull (1912).

Hitchcock (1855) reported the discovery of bones from Springfield, Massachusetts, which were discovered during blasting operations at the water shops of the United States Armory. This specimen (AM 41/109) was described by Wyman (*in* Hitchcock, 1858) but no name was applied. Subsequently Hitchcock, Jr. (1865) quoted from comments given by Sir Richard Owen and named the specimen *Megadactylus polyzelus*. *Megadactylus* was more fully described by Cope (1870) while Marsh (1882) renamed it *Amphisaurus (Megadactylus* preoccupied) but later (1885) changed it again to *Anchisaurus* when *Amphisaurus* also proved to be preoccupied.

The most productive bone locality in the Connecticut Valley was a quarry near Manchester, Connecticut, in which three well–preserved skeletons of prosauropods plus two other fragmentary specimens were discovered. These skeletons were described in several papers by Marsh (1889, 1891, 1892, 1893, 1896) and form the holotypes of *Anchisaurus major* Marsh, 1889 (YPM 208, subsequently made the type species of *Ammosaurus* Marsh, 1891); *Anchisaurus colurus* Marsh, 1891 (YPM 1883, subsequently made the type species of *Yaleosaurus* Huene, 1932); and *Anchisaurus solus* Marsh, 1892 (YPM 209). The results of subsequent studies of this material and of AM 41/109 by Huene (1906; 1907-8; 1914a, b; 1932), Lull (1915, 1953) and Galton (1971a) are detailed below in the introduction to the systematic section (p. 77). From Marsh's notebooks Lull (1915:78, 1953:61) extracted the following data concerning the specimens from the Manchester quarry:

These specimens were found in the quarry of Mr. Charles O. Wolcott about one mile north of Buckland station in a layer about two and one-half feet thickness, and, as the quarry was then worked, somewhat above the level of the roadway.

The first specimen, the *Ammosaurus major* [YPM 208] was found in 1884, and before its value was recognized the rock containing the skull and fore quarters was built into the abutments of a bridge over Bigelow Brook, South Manchester. When the block containing the hind quarters was taken out, it was saved by Mr. Wolcott, and the news of its discovery sent to Professor Marsh by Charles H. Owen, of Buckland, by whose aid and that of T. A. Bostwick the specimen was purchased. Subsequent earnest effort failed to secure the anterior portion.

The second saurian, *Yaleosaurus (Anchisaurus) colurus* [YPM 1883], was found in the same layer, twenty feet south, in a large block of sandstone. The portion exposed showed the scapula and humerus and this had been the outer surface of the quarry for a long time. There was no record of when the adjoining block had been removed. Part of the large block was split off at New Haven, and this smaller piece contained the head and part of the neck. The rest of the skeleton (except one fore leg, one hind leg, the ends of the ischia, and the tail) was subsequently found in the main block.

The third saurian, *Anchisaurus solus* [YPM 209], was found at the same time as the second, in two small blocks which were subsequently fitted together. It was about two feet higher than, and about fifteen feet southeast of the previous specimen. This third specimen is nearly entire.

In August 1969 a red sandstone bridge over Hop Brook in south Manchester was demolished and, because of a conflict in the records (Bigelow Brook passes W–E through central Manchester; see Colton, 1965), a search for bones was organized by Ostrom (1969). The search uncovered a block with the missing lateral half of the longitudinally sectioned right femur of YPM 208 (Fig. 23B). A second block (YPM 6282) has pieces of several thoracic ribs that might be prosauropod but cannot be identified more positively than dinosaurian. This is also true for four other records of bone from the Connecticut Valley: a fragment (YPM 6281) discovered in 1875 by Solon Wiley from near Greenfield, Massachusetts (see Lull, 1953); the imperfect fragments noted by Emerson (1898) from Belchertown, Massachusetts; the natural casts described by E. Hitchcock (1841) from Ellington, Connecticut; and a large rib found by Marsh in 1894 at the Manchester quarry (see Lull, 1953) from which came YPM Nos. 208, 209, 1883, and 6282.

For completeness it should be noted that three other skeletal specimens have been reported from the Portland Arkose/Longmeadow Sandstone of

the Connecticut Valley. Talbot (1911) described the skeleton of the coelurosaurian dinosaur *Podokesaurus holyokensis*, which was found near Mount Holyoke College in South Hadley, Massachusetts. This specimen was lost when the Mount Holyoke College Museum was destroyed by fire, but Colbert (1964a) has referred this species to the genus *Coelophysis*. A second specimen (Boston Society of Natural History No. 13656) is also referred to *Coelophysis* by Colbert and Baird (1958). This block with a natural cast of the pubis and tibia was probably found in Portland, Connecticut and was first reported by Rogers (1864). The third specimen is a skeleton from near Longmeadow, Massachusetts, which was described by Emerson and Loomis (1904) as *Stegomus longipes* but which Huene (1922) made the type species of *Stegomosuchus*. *Stegomosuchus* has long been regarded as a thecodont, but Walker (1968, 1970) suggested that it is a primitive crocodile related to *Protosuchus* (see also Galton, 1971a). A small tooth referable to *Coelophysis* was collected in 1970 by B. Cornet and N. G. McDonald (personal communication) from black shale in a stream cut in the Shuttle Meadow Formation, northeast side of Totoket Mountain, North Guilford, Connecticut (see Cornet et al., 1973, locality 1).

The remaining North American material of prosauropod dinosaurs comes from the Navajo Sandstone of the Navajo Indian Reservation, northeastern Arizona. Brady (1935, 1936) gave a preliminary description of a partial skeleton (MNA G2 7233), which he referred to the genus *Ammosaurus*. In a recent paper (Galton, 1971a) I have described this specimen and another (UCMP 82961) of *Ammosaurus* plus the armor and pes (UCMP 61299) of the primitive crocodile *Protosuchus*. The last two skeletons were collected by Camp who described the only other skeletal remains reported from the Navajo Sandstone, the coelurosaurian dinosaur *Segisaurus halli* Camp, 1936.

Despite the abundance of footprints from Jura-Triassic formations of North America, those of prosauropods are almost completely lacking. A few of these ichnite genera from the Connecticut Valley have been identified as those of prosauropods, with Lull (1953) listing *Anchisauripus* and *Otozoum* whereas Haubold (1969) lists *Anomoepus, Apatichnus*, and *Otozoum*. However, the manus (Figs. 17C, 36A) and pes (Figs. 22E, 29D, 38A) of prosauropods are very distinctive and none of these ichnite genera show the combination of characters diagnostic of a prosauropod trackway. The footprints of *Anchisauripus* were probably made by a coelurosaurian dinosaur (a small theropod) (Baird, 1957:458-461, 504-505; Colbert and Baird, 1958:9; Galton, 1970a, 1971a); those of *Anomoepus* and *Apatichnus* by ornithopod dinosaurs (Lull, 1904, 1915, 1953), and those of *Otozoum* by a lone descendant of the chirotheriid thecodont stock (Baird, 1957:485; Colbert and Baird, 1958:10). Baird (as cited by Galton, 1971a) reports a trackway (MNA G2 7092) from the Navajo Sandstone of Arizona which was undoubtedly made by a prosauropod walking quadrupedally.

The age of the upper part of the Portland Formation of the Connecticut

Valley has long been regarded as Upper Triassic (Rhaetic). However, recent correlations using evidence from spores and pollen indicate that these beds are Lower Jurassic in age (Cornet et al., 1973) and perhaps no older than Pleinsbachian (Cornet and Traverse, 1975). Because of the similarities of the reptilian faunas (Galton, 1971a), the Navajo Sandstone of northeastern Arizona is probably about the same age (Cornet and Traverse, 1975) rather than Upper Triassic (Galton, 1971a).

3. DESCRIPTION OF SPECIMENS

In the historical survey above and in the descriptions that follow I have avoided any detailed discussion of the systematics because this subject is considered in a separate section (p. 77). All the specimens have been described previously and in the case of those from the Connecticut Valley several different names were used (Table 1). A list of the synonymies from the primary literature precedes the description of the specimen concerned.
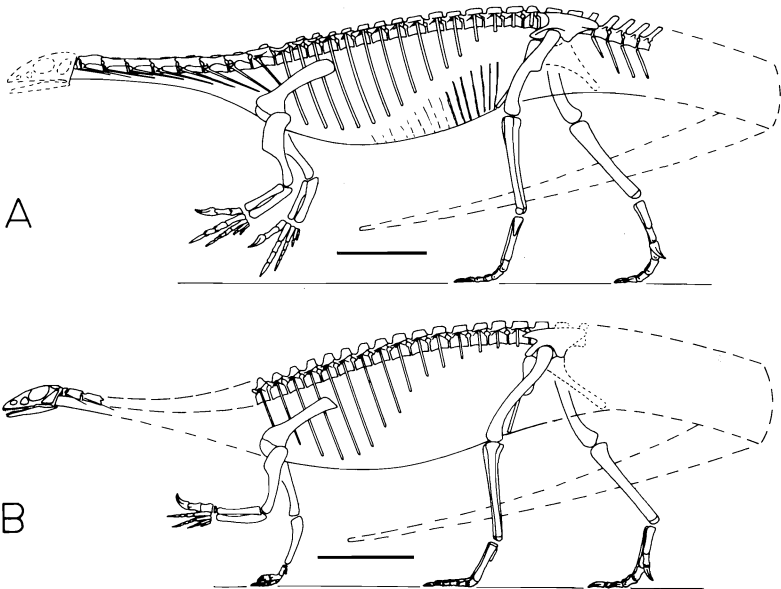
FIG. 1. Skeletal reconstructions of anchisaurid prosauropods. *A, Efraasia diagnostica*, from the Stubensandstone (Upper Triassic) of Germany, based on SMNS 12667 and 12668; *B, Anchisaurus polyzelus* from the Connecticut Jurassic, based on YPM 1883 with proportions of femur and fibula adjusted to agree with AM 41/109. Tails after *Plateosaurus* (Fig. 2B), and diagrammatically folded over; horizontal lines represent 20 cm; from Galton (1973a).

TABLE 1. Synonymy of the Connecticut Valley prosauropods.

Author	Marsh 1896	Huene 1906	Lull 1915	Huene 1932	Lull 1953	Galton 1971a
Specimen						
AM 41/109[1]	*An.*ᵀ *polyz.*ᵀ	*Th. polyz.*ᵀ	*An.*ᵀ *polyz.*ᵀ	*Th. polyz.*ᵀ	*An.*ᵀ *polyz.*ᵀ	*An.*ᵀ *polyz.*ᵀ
YPM 1883[2]	*An. colurus*ᵀ	*An. colurus*ᵀ	*An. colurus*ᵀ	*Y.*ᵀ *colurus*ᵀ	*Y.*ᵀ *colurus*ᵀ	*An. polyz.*
YPM 208[3]	*Am.*ᵀ *major*ᵀ	*Am.*ᵀ *major*ᵀ	*Am.*ᵀ *major*ᵀ	*Am.*ᵀ *major*ᵀ	*Am.*ᵀ *major*ᵀ	*Am.*ᵀ *major*ᵀ
YPM 209[4]	*An. solus*ᵀ	*An. ? solus*ᵀ	*An. solus*ᵀ	*Am. solus*ᵀ	*An. solus*ᵀ	*Am. major*
YPM 2125	–	–	*An. colurus*	*Y. colurus*	*Y. colurus*	prosauropod

Abbreviations: *Am.* = *Ammosaurus; An.* = *Anchisaurus; polyz.* = *polyzelus;* T = holotype; *Th.* = *Thecodontosaurus Y.* = *Yaleosaurus.*

[1] *Megadactylus polyzelus* E. Hitchcock, Jr. 1865; *Amphisaurus* Marsh 1882; *Anchisaurus* Marsh 1885.
[2] *Anchisaurus colurus* Marsh 1891; *Yaleosaurus* Huene 1932.
[3] *Anchisaurus major* Marsh 1889; *Ammosaurus major* (Marsh 1891).
[4] *Anchisaurus solus* Marsh 1892.
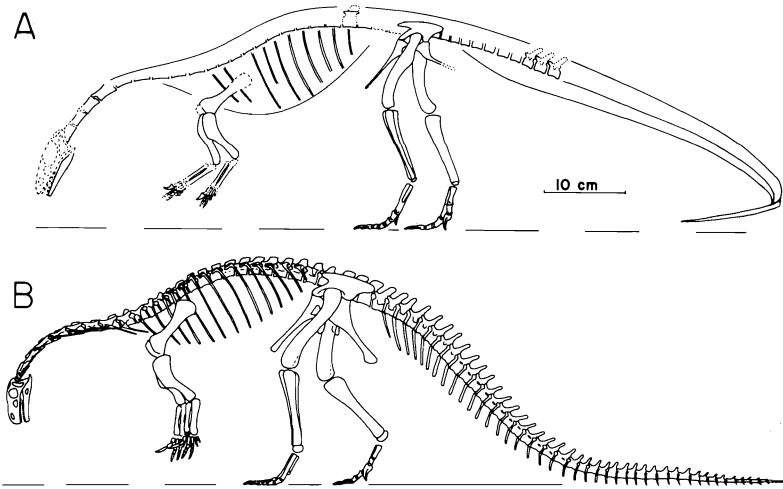
FIG. 2. Skeletal reconstructions of plateosaurid prosauropods. *A, Ammosaurus major* from the Connecticut Jurassic, based on YPM 209 with pelvis and pes from YPM 208; head outline adapted from YPM 1883 and tail from *Plateosaurus*. *B, Plateosaurus*, based on AMNH 6810, original about 6 m long; from Galton (1971a). For photograph see Colbert (1961, pl. 28).

As summarized elsewhere (Galton, 1971a), I recognize two monospecific genera (for diagnoses see p. 82, 88) of North American prosauropods: the slender-footed *Anchisaurus polyzelus* (holotype AM 41/109, referred specimen YPM 1883; Fig. 1B) and the broad-footed *Ammosaurus major* (holotype YPM 208, referred specimen YPM 209; Fig. 2A) with the material from Arizona (MNA G2 7233, UCMP 82961) as *Ammosaurus* cf. *major*. The principal measurements of the bones of these specimens are given in Tables 2 to 4. In the figures, labels in capitals designate bones and those in lowercase indicate structures.

Anchisaurus polyzelus (Hitchcock, Jr.)
Specimen 1, AM 41/109 (Figs. 3, 5-10)

IDENTIFICATION. This specimen is the holotype of *Megadactylus polyzelus* Hitchcock, Jr., 1865:40, the type species of the genus *Anchisaurus* Marsh, 1885:169 (for discussion of systematics see p. 77).

TABLE 2. Measurements of specimens of *Anchisaurus polyzelus* — Vertebrae. All measurements in mm.

Vertebrae		L	H	W_a	W_m	W_p	Rib
YPM 1883							
Cervical	2	33	20	9	–	–	–
	3	48	18	–	–	11	–
Dorsal	1	–	–	–	–	–	–
	2	(24)	47	–	9	19	–
	3	30	–	18	–	18	160
	4	–	–	–	–	–	180
	5	30	–	–	8	20	205
	6	34	–	18	9	20	235
	7	35	–	–	10	19	205
	8	35	–	19	10	19	195
	9	35	40	19	10	20	185
	10	38	–	20	9.5	21	153
	11	36	–	20	9.5	21	+120
	12	37	–	21	10	22	133
	13	37	50	–	–	–	+ 55
	14	–	–	–	–	–	–
	15	42	–	–	–	(27)	–
Sacral	1	38	–	28	13	26	36
	2	–	–	–	–	–	23

Abbreviations: H = greatest height; L = length of centrum; RL = length of rib as measured along the curve; W_a = width of centrum anteriorly; W_m = minimum width of centrum; W_p = width of centrum posteriorly; ( ) = estimate + = more than.

PREVIOUS DESCRIPTIONS OF AM 41/109.
Unnamed, Hitchcock, 1855:416; 1858:186–187.
Megadactylus polyzelus Hitchcock, Jr., 1865:39–40, pl. 9, fig. 6; Cope, 1870:122A–G, pl. 13.
Amphisaurus (polyzelus) Marsh, 1882:84.
Anchisaurus (polyzelus) Marsh, 1885:169.
Anchisaurus polyzelus (Hitchcock, Jr.) Marsh, 1892, pl. 16, fig. 3, pl. 17, fig. 6; 1896:147, pl. 3, figs. 4–5; Lull, 1915:119–130, figs. 14–17; 1953: 99-107, figs. 12–14a.
Thecodontosaurus polyzelus (Hitchcock, Jr.) Huene, 1906:19–22, figs. 10, 10a; 1914b:75–77, figs. 23–24; 1932:116–117.

LOCALITY. Water shops, U.S. Armory, Springfield, Massachusetts.

HORIZON. Longmeadow Sandstone, from the upper (Portland) beds of sandstones, etc. of the Newark Series.

TABLE 3. Measurements of specimens of *Anchisaurus polyzelus*. Limbs and girdles. All measurements in mm.

		L	W_p	W_m	W_d
YPM 1883					
Scapula		144	50	18	–
Humerus		150	50	–	–
Radius		95	19	10	15
Ulna		105	30	–	–
Metacarpal	1	28	22	14	17
	2	36	9	7	11
	3	34	–	7	8
	4	26	10	5	8
	5	16	10	–	–
Pubis		190	35	–	30
Ischium		–	55	–	–
Ilium		–	84[a]	30[b]	35[c]
Femur		211	–	–	147
Tibia		145	47	17	34
Fibula		150	32	11	24
Metatarsal	1	63	–	–	16
	2	88	18	10	18
	3	98	–	13	21
	4	89	–	13	11
	5	44	21	–	–
AM 41/109					
Metacarpal	1	19	16	–	10
	2	28	7	5	–
	3	25	5.5	4	6
	4	20	–	4	–
	5	14	8	–	7
Femur		178	40	20	42
Tibia		–	48	–	14
Fibula		158	18	12	18
Metatarsal	4	72	19	8	15

Abbreviations: a = width across pubis and ischiadic heads; b = minimum height above acetabulum; c = length of anterior process; L = greatest length; W_d = maximum width of distal end; W_m = minimum width of shaft; W_p = maximum width of proximal end.

MATERIAL. As a result of the blast which exposed the bones and of subsequent losses the specimen (Figs. 3–11) now includes 11 vertebrae, an incomplete scapula, an almost complete manus, the ischial rods and an incomplete hind limb.

VERTEBRAL COLUMN. Further preparation shows that the "ventral view" of a cervical vertebra given by Huene (1914b, fig. 23) is the posterolateral view

TABLE 4. Measurements of specimens of *Ammosaurus major*. All measurements in mm.

			L	W_p	W_m	W_d	L_u
Right pes	YPM 208						
Metatarsal		1	74	26	15	29	55
		2	110	22	18	34	51
		3	120	–	17	32	49
		4	110	–	–	–	32
Left pes	YPM 208						
Metatarsal		1	72	–	16	31	48
		2	114	18	17	30	–
		3	135	27	18	27	–
		5	58	–	–	–	–

			L_r	L_u	L_l	L_{lu}	U
Right pes	MNA G2 7233						
Metatarsal		1	83	67	–	–	(60)
		2	128	55	–	–	(50)
		3	(143)	45	–	41	45
		4	133	–	125	35	39
		5	(65)	–	70	24	–
Left pes	YPM 209						
Metatarsal		1	28				
		2	41				
		3	48				
		4	43				

			L	L_{lu}
Left Manus	UCMP 92961			
Metacarpal		1	34	66
		2	–	37
		3	42	12
		4	39	–
		5	23	–

Length of centra	YPM 209		
Cervical		5	22
		6	21
		9	19
		10	18
Dorsal		1	13
		4	14
		6	17
		7	17
		8	17
		9	18
		10	18
		11	18
		12	19
		13	19
Caudal		8	7

Abbreviations: L = Length; L_l = length of left metatarsal; L_r = length of right metatarsal; L_{lu} = length of left ungual; L_u = length of right ungual; W_d = maximum width of distal end; W_m = minimum width of shaft; W_p maximum width at proximal end; U = length of ungual of pes of UCMP 92961; ( ) = estimate.

of the neural arch of the second sacral vertebra (Figs. 3E, 3G). There is a natural mold of the proximal part of a cervical rib (Fig. 5A) plus two incomplete ribs (Fig. 5B) which are from either the posterior part of the neck or the anterior part of the trunk. An isolated neural arch is probably that of a dorsal vertebra from the middle part of the series. The left postzygapophysis (Figs. 3B, 3C) has an accessory articular surface, the zygosphene, as in YPM 1883 (Fig. 15I), *Massospondylus* (Figs. 4B, 4E) and *Plateosaurus* (Huene, 1926). Most of the zygosphene surface is flat, but anteriorly it becomes concave longitudinally and transversely. Zygantra were presumably present as in *Massospondylus* (Fig. 4A) and *Plateosaurus* (Huene, 1926) but the prezygapophyses are not preserved (Fig. 3C).

The vertebral centrum (Fig. 5C) regarded by Cope (1870, fig. 5; see Lull, 1953, fig. 12d) as that of a dorsolumbar vertebra and by Huene (1914b, fig. 2G) as that of a caudal vertebra is probably from a dorsal vertebra. In ventral view (Fig. 5C) the centrum is elongate and resembles those of YPM 1883 (Figs. 11, 15L). The preserved end surface is gently concave and there is no trace of an articulation for a chevron. The vertebral centrum (Fig. 5F) regarded by Cope (1870, fig. 6; see Lull, 1953, fig. 12b) as that of a sacral vertebra may be from the last dorsal vertebra. The anterior surface is gently concave (Fig. 5F), the pleurocoel is well developed (Fig. 5G) and the flat posterior end (Fig. 5H) is expanded (Figs. 5G–J). The
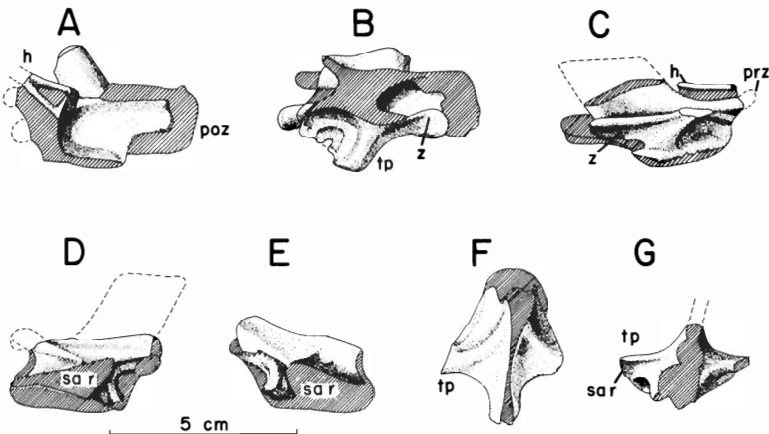

FIG. 3. *Anchisaurus polyzelus*. AM 41/109. Neural arches × 0.5. *A–C*, a middorsal vertebra: *A*, dorsal view; *B*, ventral view; *C*, lateral view of right side; *D–G*, second sacral vertebra: *D*, lateral view of left side; *E*, lateral view of right side; *F*, dorsal view; *G*, posterior view. Abbreviations: *h* = proximal part of haemal arch of a caudal vertebra; *poz* = postzygapophysis; *prz* = prezygapophysis; *sar* = surface for sacral rib 2; *tp* = transverse process; *z* = zygosphene. Matrix indicated by diagonal pattern.
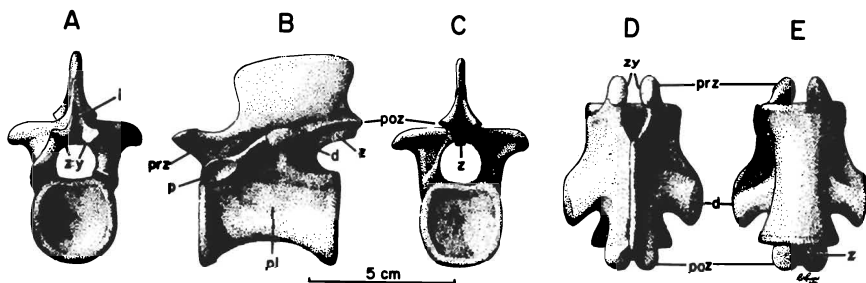
FIG. 4. *Massospondylus* sp., AMNH 5624. Middorsal vertebra, slightly less than × 0.4. *A*, anterior view; *B*, lateral view; *C*, posterior view; *D*, dorsal view; *E*, ventral view. Abbreviations: *d* = diaphysis; p = paraphysis; *pl* = pleurocoel; *zy* = zygantrum; other abbreviations as in Figure 3. This specimen is from the Red Beds of Fouriesburg, Orange Free State, South Africa, and it is listed in Broom (1915, p. 162) as *Aetonyx palustris*. The specimen consists of several dorsal vertebrae and a manus (Galton and Cluver, in press, fig. 7P). Several bones of the manus of a much larger individual now have a separate specimen number (AMNH 4981).

form of this centrum is similar to that of the last dorsal vertebra of *Efraasia diagnostica* (SMNS 12667; Galton, 1973a), but it might be the third sacral vertebra. The short centrum regarded by Huene (1914b, fig. 24) as that of a dorsal vertebra could not be located. As figured the height and length are about equal at 2 cm and this length is rather short for a dorsal vertebra (cf. Figs. 5C, 5G); this centrum was probably from an anterior caudal vertebra (cf. Fig. 5L).

The centrum of the first sacral vertebra is distorted and has been restored (Figs. 5C, 5E). The facet for the first sacral rib is set well forward (Fig. 5E) as in YPM 1883 (Fig. 15K), *Ammosaurus* (Fig. 31B) and *Plateosaurus* (Huene, 1926). The neural arch (Figs. 3D–G) is probably from a sacral vertebra. There is no well-formed ventral surface to either of the transverse processes (Figs. 3D, 3E) which, apart from being skewed slightly sideways, are symmetrical in posterior view (Fig. 3G). The transverse processes of the first sacral vertebra are set more anteriorly and are more anteriorly directed in *Ammosaurus* (Fig. 31A), *Thecodontosaurus* (Huene, 1914b, fig. 39a), and *Plateosaurus* (Huene, 1926, pl. 2, fig. 3), whereas the neural arch of the third sacral vertebra of *Ammosaurus* and of *Plateosaurus* is quite different. This neural arch (Figs. 3D, 3E) is identified as that of the second sacral vertebra; it is quite similar to those of *Ammosaurus* (Fig. 31A), *Thecodontosaurus*, and *Plateosaurus*. One difference is that there is only a slight anterior ridge to the transverse process (Figs. 3D, 3F) as in YPM 1883, whereas in *Ammosaurus* and *Thecodontosaurus* there is a sharp edge with a considerable excavation of the neural arch ventrally.
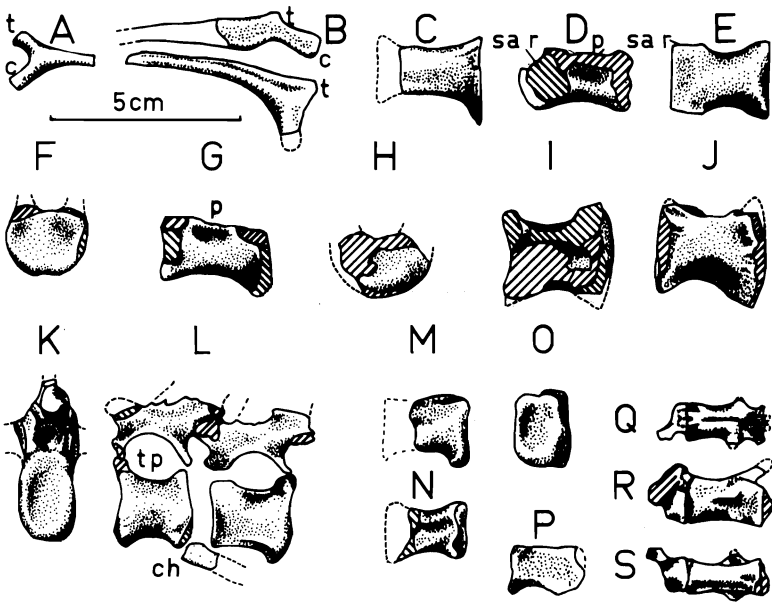
FIG. 5. *Anchisaurus polyzelus.* AM 41/109. Vertebrae × 0.5. *A*, impression of the proximal part of a cervical rib; *B*, two ribs from the right side in lateral view; *C*, incomplete centrum of a dorsal vertebra in ventral view; *D*, centrum of first sacral vertebra in lateral view; *E*, as *D* in ventral view; *F–J*, centrum of last dorsal vertebra: *F*, anterior view; *G*, lateral view of left side; *H*, posterior view; *I*, dorsal view; *J*, ventral view; *K*, proximal caudal vertebra in anterior view (*cf. L*); *L*, two anterior caudal vertebrae in lateral view; *M–O*, incomplete centrum of an anterior caudal vertebra, *M*, lateral view; *N*, ventral view; *O*, ? posterior view; *P*, dorsal view of an isolated right transverse process from an anterior caudal vertebra; *Q–S*, two incomplete distal caudal vertebrae, *Q*, dorsal view; *R*, lateral view of left side; *S*, ventral view. Abbreviations: *c* = capitulum; *ch* = chevron; *p* = pleurocoel; *sa r* = surface for sacral rib; *tp* = surface for transverse process. Broken bone indicated by diagonal pattern.

Two articulated caudal vertebrae (Figs. 5K, 5L) lack transverse processes, but there is an isolated transverse process (Fig. 5P). It is apparent that the transverse processes were not ankylosed to the neural arch and this indicates that the specimen probably represents a young or subadult animal. The other caudal vertebrae (Figs. 5Q–S) were from the posterior third of the tail.
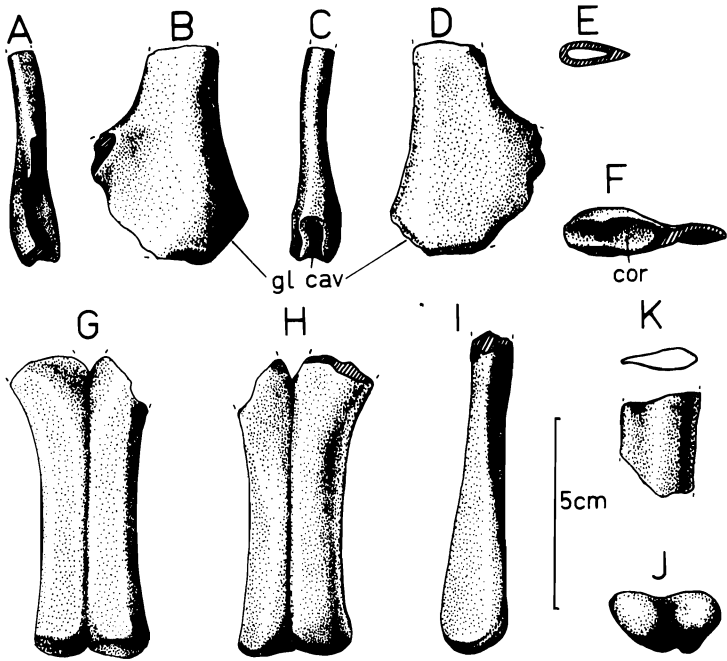
FIG. 6. *Anchisaurus polyzelus*. AM 41/109. Scapula and ischia × 0.5. Left scapula in *A*, anterior view; *B*, lateral view; *C*, posterior view; *D*, medial view; *E*, section of shaft; *F*, ventral edge. Ischial rods in *G*, dorsal view; *H*, ventral view; *I*, lateral view of left ischial rod; *J*, distal view of ischial rods; *K*, ? piece of right ischium. Abbreviations: *cor* = surface for coracoid; *gl cav* = glenoid cavity. Broken bone indicated by diagonal pattern.

PECTORAL GIRDLE AND FORELIMB. The ventral part of the left scapula (Figs. 6A–F) was figured as the proximal part of the ischium by Marsh (1892, pl. 17, fig. 6; 1896, pl. 3, fig. 4), Huene (1914b, fig. 29), and Lull (1915, fig. 17; 1953, fig. 14a). Most of the anterior third of the bone is very thin; the more massive posteroventral part carried a sutural surface for the coracoid and the glenoid (Figs. 5B–D, 5F), the exact form of which cannot be determined.

The block containing the right manus was split with bones and natural molds on each part (Figs. 7L, 7M). Sections (Figs. 7B, C, F) show that the radius and ulna have very thin walls. The large first distal carpal and the smaller second distal carpal are sectioned (Figs. 7L, M). Comparisons with casts of the manus of *Plateosaurus* (UT1) show that the metacarpals and digits were reorientated during preservation as follows: the first digit was rotated around its long axis through 180°, the phalanges of the second digit

were rotated through 90°, and those of the third digit through 180°. The first digit (Figs. 7A, G, L) shows various features typical of prosauropods with the ungual phalanx directed away from the other digits rather than towards them as shown by Marsh (1892, pl. 16, fig. 3; 1896, pl. 3, fig. 5; see Lull, 1953, fig. 13). The exact form of the distal ends of metacarpals 2–4 cannot be determined, but they are slender, resembling those of YPM 1883 (Figs. 17C, 18), *Thecodontosaurus* (YPM 2195) and *Efraasia* (Galton, 1973a).

PELVIC GIRDLE AND HIND LIMB: Distally the subtriangular ischial rods (Figs. 6G–J) are separated by a slight groove dorsally and ventrally (Fig. 6J). The dorsal groove becomes wider and deeper more proximally so that contact between the rods becomes progressively reduced. The dorsal and lateral edges are gently convex and form an edge that becomes progressively more acute proximally. There is a small piece of bone (Fig. 6K) that might be part of the anterior plate of the pubis (Huene, 1914b), part of the shaft of the right ischium, or part of the left scapula.

The femur is in four pieces, the broken ends of which were ground and polished so that there are no contacts between the pieces. However, the curves of the pieces can be matched to give a reasonably accurate reconstruction of the original bone (Fig. 8). The femur is hollow with thin walls (Figs. 8F–H) as is also the case for the tibia (Figs. 9F, G), fibula (Fig. 9K) and metatarsals (Fig. 10M). The transversely oriented depression on the rough textured proximal end of the head (Fig. 8E) appears to be natural and in life this surface was probably covered by cartilage. Immediately ventral to the head the shaft is roughly oval in cross section with a greatly convex medial edge and a sharp lateral edge. The latter becomes more gently curved just above the fourth trochanter (Fig. 8F) and disappears below it (Fig. 8G). Immediately posterior to the lesser trochanter the surface is transversely concave so that the lesser trochanter is a sharp-edged ridge. The proximal part of the fourth trochanter is thick with a gently convex edge (Figs. 8B, C), but more distally it becomes thinner with a sharp edge. Medially there is a very well-defined depression that extends from the posterior surface of the trochanter onto the adjacent part of the shaft (Fig. 8C). This area has prominent surface markings and was obviously for the attachment of a muscle, probably the M. caudifemoralis longus, which originates from the sides of the tail and inserts onto a depression comparable to that on the femur of the alligator. The M. caudifemoralis brevis probably originated from the first few anterior caudal vertebrae and inserted onto the posterior surface of the fourth trochanter (Fig. 8B) and more proximally onto the medial surface. The large fourth trochanter of prosauropods probably increased the lever arm of the M. caudifemoralis brevis during the first phase of femoral retraction (see discussion of ornithopod dinosaurs in Galton, 1969). The more sheet-like
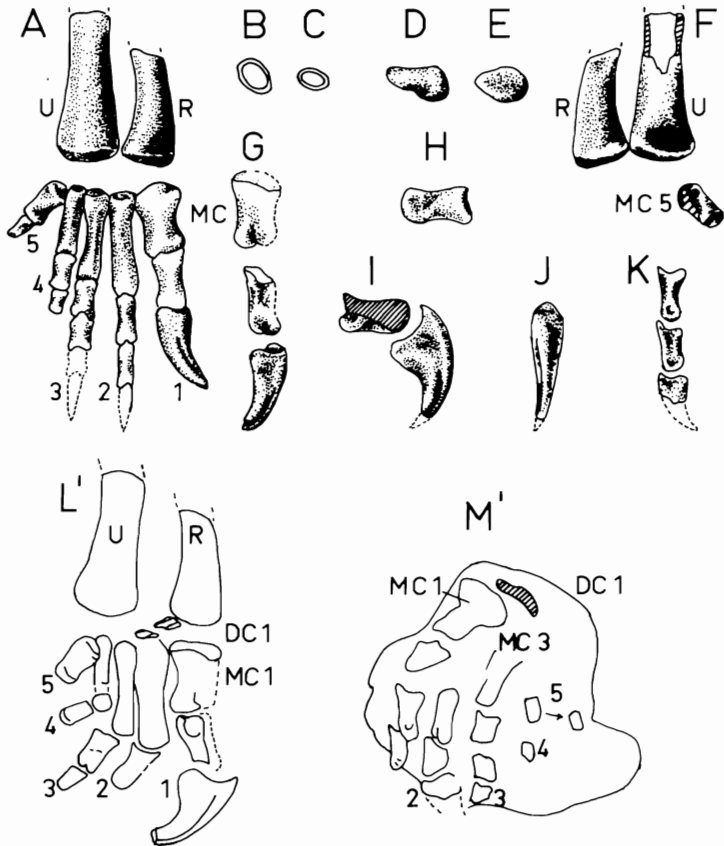
FIG. 7. *Anchisaurus polyzelus*. AM 41/109. Right manus × 0.5. *A*, restored manus in dorsal view; *B*, sectioned shaft of ulna; *C*, sectioned shaft of radius; *D*, distal end of ulna; *E*, distal end of radius; *F*, ventral view of radius, ulna and metacarpal 5; *G*, disarticulated first digit in ventral view; *H*, medial view phalanx 1 of digit 1; *I*, phalanges of digit 1 in lateral view; *J*, first ungual phalanx in dorsal view; *K*, phalanges of digit 2 in medial view; *L*, stereophotograph of manus as preserved on main block with explanatory outline (*L'*); *M*, stereophotograph of counterblock to *L* with explanatory outline (*M'*). Abbreviations: *DC*, distal carpal; *MC* = metacarpal; *R* = radius; *U* = ulna. Broken bone indicated by diagonal pattern.
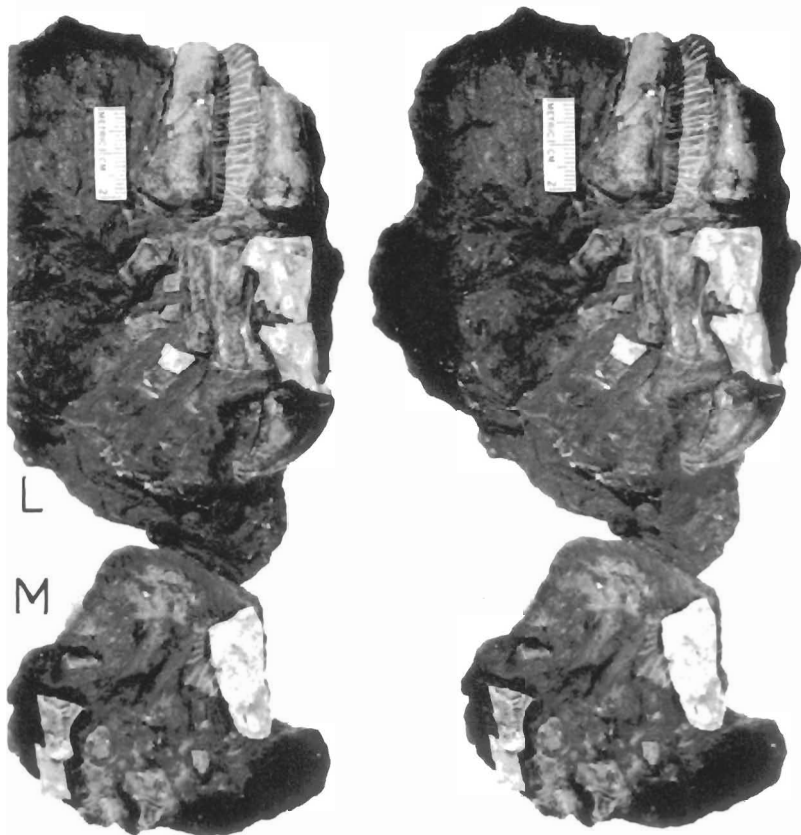
outer condyle (Fig. 8B) continues proximally onto the shaft as a well-defined ridge (Figs. 8A, B).

The proximal part of the tibia is in two pieces, the curves of which have been matched as shown (Figs. 9A–D, K). The proximal end has been crushed slightly so that the acuteness of the anterior cnemial crest (Figs. 9D, E) is somewhat exaggerated. The lateral surface (Fig. 9A) has two concavities (Fig. 9E), a large one backing the cnemial crest and a smaller one between the outer and inner condyles. Both concavities merge into the convex surface of the shaft more distally.

The pieces of matrix still attached to the proximal and distal ends of the fibula have natural molds into which the two parts of the tibia fit. Consequently the original length of the fibula can be reconstructed (Figs. 9H–K) at about 160 mm. The tibia was presumably the same length as the fibula as in *Plateosaurus* (Huene, 1926) and *Efraasia* (Galton, 1973) so it was
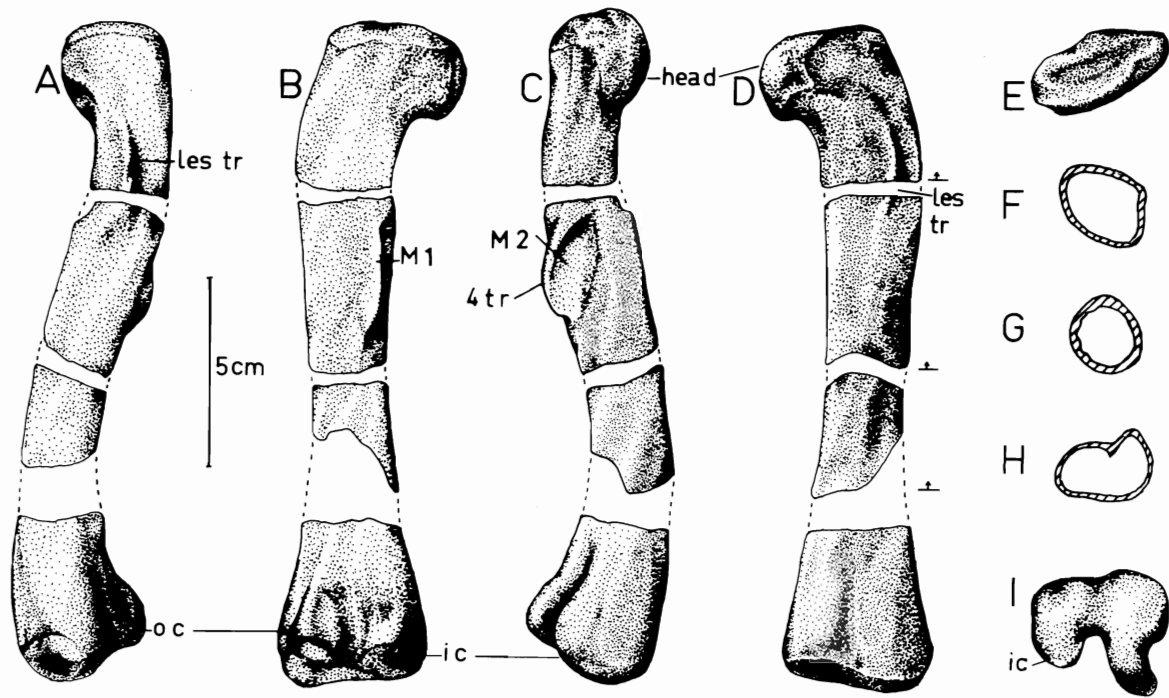
FIG. 8. *Anchisaurus polyzelus*. AM 41/109. Left femur × 0.5. *A*, lateral view; *B*, posterior view; *C*, medial view; *D*, anterior view; *E*, proximal end; *F–H*, sections through the shaft as indicated on *D*; *I*, distal end. Abbreviations: *i c* = inner condyle; *les tr* = lesser trochanter; *M1* = M. caudifemoralis brevis; *M2* = M. caudifemoralis longus; *oc* = outer condyle; *4tr* = fourth trochanter.

shorter than the femur at about 180 mm. The planes of expansion of the proximal (Fig. 9I) and distal (Fig. 9H) ends of the fibula are perpendicular to each other. The medial surface of the distal part (Fig. 9L) has a diagonally inclined sharp edge which merges with the shaft more proximally.

The calcaneum is lost and its outline (Figs. 9J, K) is taken from Cope (1870, pl. 13, fig. 4). As preserved the fourth metatarsal of the left pes is acutely flexed with respect to the fibula (Figs. 9J, K). The dorsoventral compression of the proximal end of metatarsal 4 (Figs. 10A–F) is an artifact of preservation. An isolated proximal end (Figs. 10H–M) is probably part of the second metatarsal of the right foot, but it could be from the third metatarsal of the left foot. The first phalanx of the third digit of the left pes is visible in ventral view (Fig. 10G) and fragments of two other phalanges of this foot are visible. Both metatarsals and phalanges are quite slender and in this respect resemble those of YPM 1883 (Figs. 12, 22E), *Anchisaurus capensis* (Broom, 1906, 1911; Galton and Cluver, in press), *Efraasia* (Galton, 1973a), and *Thecodontosaurus* (Galton, 1973a).

Anchisaurus polyzelus
Specimen 2, YPM 1883 (Figs. 1B, 11-22)

IDENTIFICATION. This specimen is referred to *Anchisaurus polyzelus*, it is the holotype of *Anchisaurus colurus* Marsh, 1891:267 which is the type species of the genus *Yaleosaurus* Huene, 1932:122.


PREVIOUS DESCRIPTIONS.
Anchisaurus colurus Marsh, 1891:267–268; 1892:543–545, pl. 15, pl. 16, figs. 1, 2; 1893:169–170, pl. 6; 1896:148, pl. 2, figs. 1–3, pl. 3, figs. 1, 2, pl. 4; Huene, 1906:6–13, figs. 1–6; pls. 1–3; 1914b:69–72, figs. 1–11; Lull, 1912:414, figs. 2, 3; 1915:130–144, figs. 18–21, pls. 4, 10.
Yaleosaurus colurus (Marsh) Huene, 1932:119–122, pl. 14, fig. 1, pl. 54, fig. 3; Lull, 1953:107–120, figs. 15–18, pl. 4.
Anchisaurus polyzelus (Hitchock, Jr.) Galton, 1971a:782, fig. 7C; 1973a, figs. 1F, H, M, O, P, S.

LOCALITY. Manchester, Connecticut, in the quarry of Charles O. Wolcott, about one mile north of Buckland Station.

HORIZON. High in the upper (Portland) beds in coarse, red arkose, near top of the Newark Series. (For age see p. 6.)
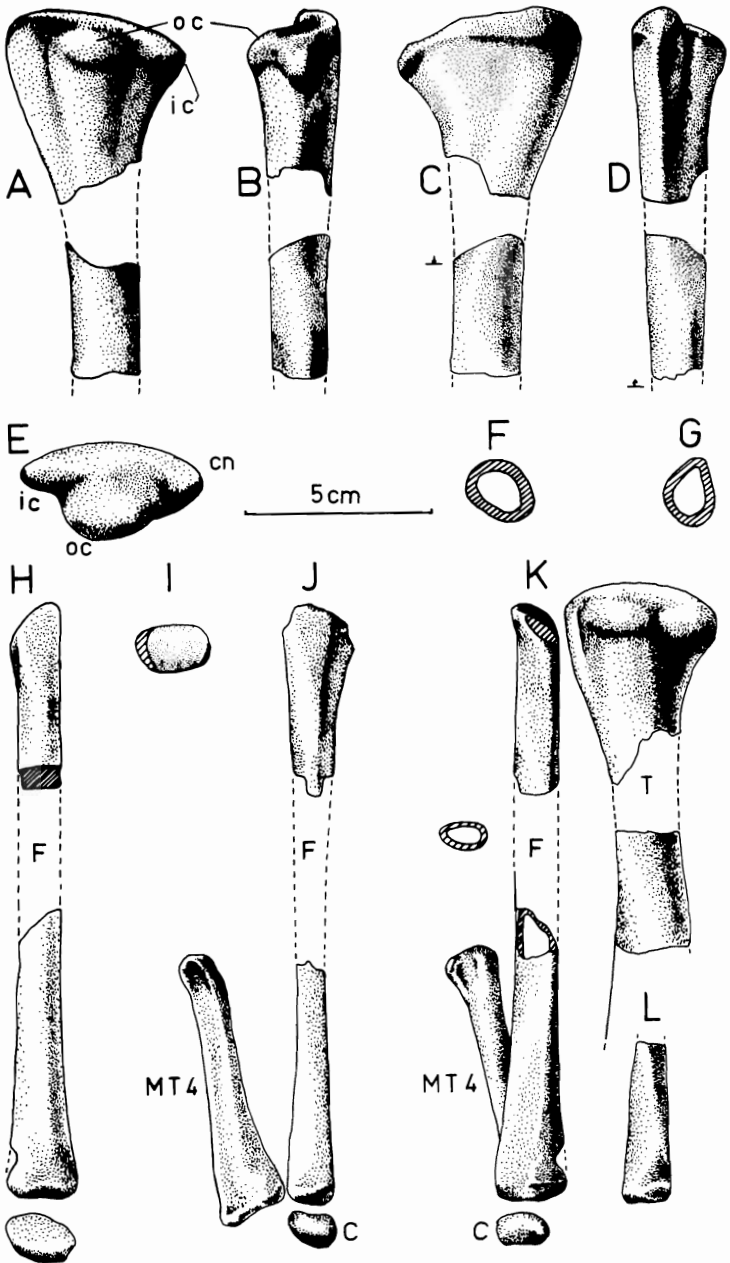
MATERIAL. This is the best-preserved skeleton of a prosauropod from North America and, apart from the specimen of *Efraasia diagnostica* from Germany (see Galton, 1973a), it is the only reasonably complete skeleton of a slender-footed prosauropod (Figs. 1B, 11–22) described to date. The elements missing are cervical vertebrae 4 to 10, the tail, the left forelimb (apart from the proximal part of humerus), most of both ischia, the left ilium and the left hind limb. There is no record of the relative positions of the skull, cervical vertebrae, and the main block but, judging from the horizontal position of the lower arm, femur and pes, it is probably the
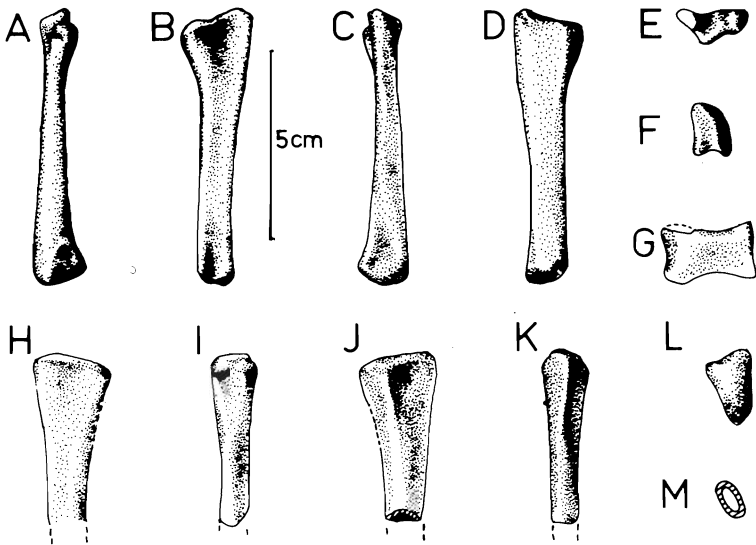

FIG. 10. *Anchisaurus polyzelus*. AM 41/109. Metatarsals × 0.5. Left fourth metatarsal in *A*, lateral view; *B*, ventral view; *C*, medial view; *D*, dorsal view; *E*, proximal end; *F*, distal end; *G*, ventral view of phalanx 1 of digit 3. Proximal half of right second metatarsal in *H*, lateral view; *I*, ventral view; *J*, medial view; *K*, dorsal view; *L*, proximal end; *M*, section through shaft.

FIG. 9. *Anchisaurus polyzelus*. AM 41/109. Left tibia and fibula × 0.5. Left tibia in *A*, lateral view; *B*, posterior view; *C*, medial view; *D*, anterior view; *E*, proximal view; *F*, *G*, sections through shaft as indicated in *C* and *D*. Left fibula in *H*, anterior view with distal end; *I*, proximal end; *J*, lateral view with calcaneum and metatarsal 4; *K*, posterior view as *J* plus tibia; *L*, medial view of distal part of fibula. Abbreviations: *C* = calcaneum; *F* = fibula; *MT* = metatarsal; *T* = tibia; *cn* = cnemial crest; *ic* = inner condyle; *oc* = outer condyle.
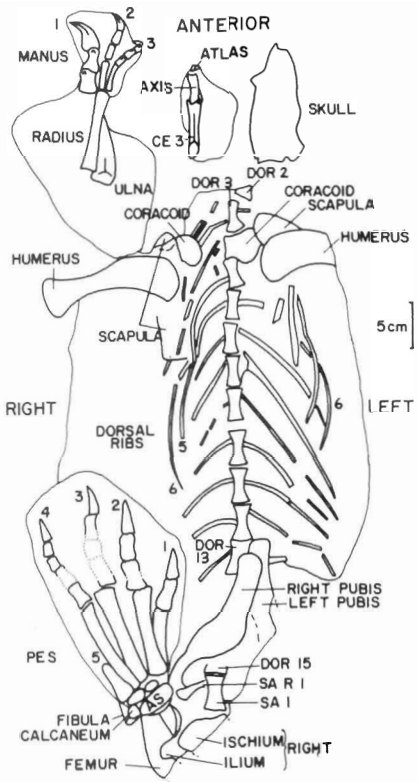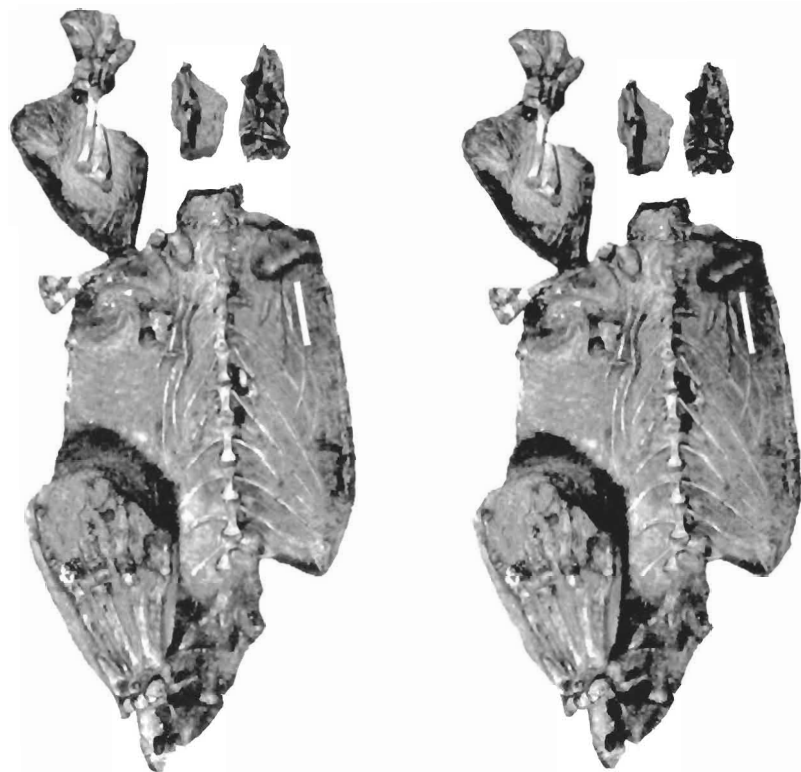
FIG. 11. *Anchisaurus polyzelus.* YPM 1883. Stereophotograph of specimen, with outline drawing.
Abbreviations: *AS* = astragalus; *CE* = cervical vertebra; *DOR* = dorsal vertebra; *SA 1* = sacral vertebra 1;
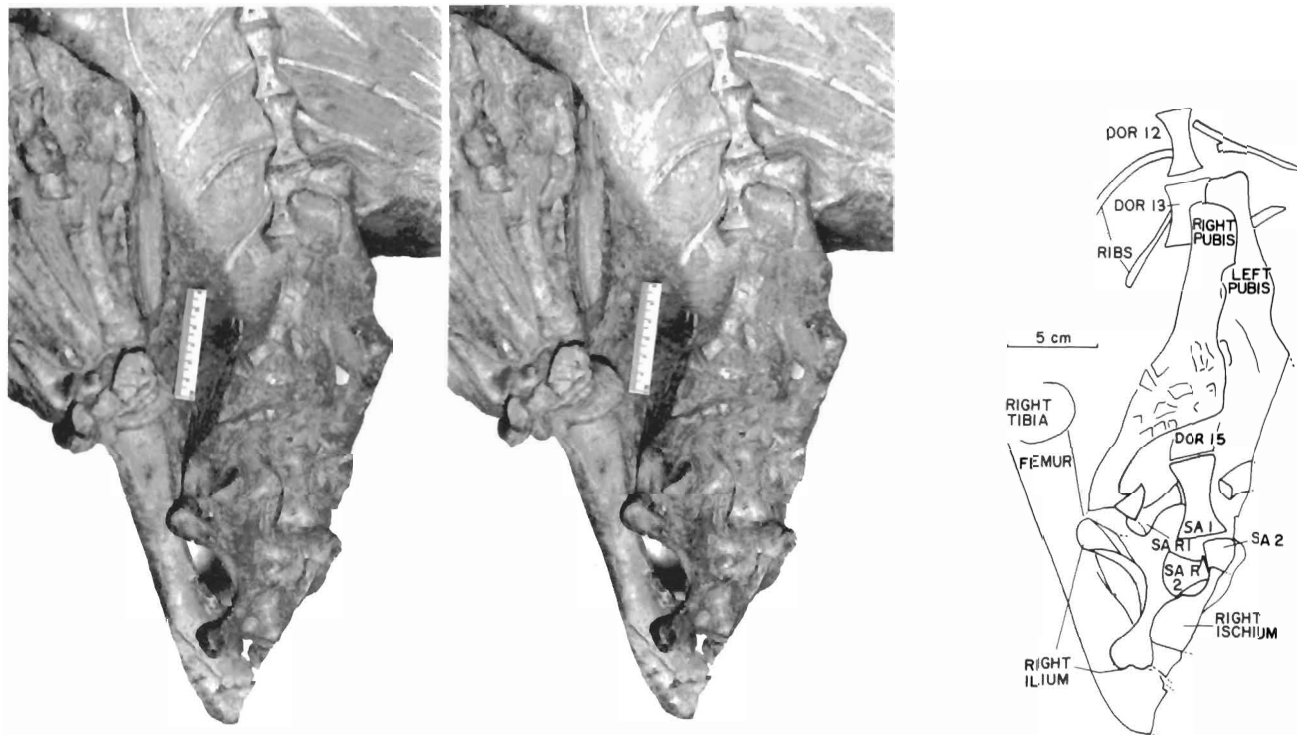*SA R 1* = first sacral rib.

FIG. 12. *Anchisaurus polyzelus.* YPM 1883. Stereophotograph, with outline drawing, to show details of posterior region of main block. Abbreviations: *DOR* = dorsal vertebra; *SA* = sacral vertebra; *SAR* = sacral rib.

lower surface of the main block that is exposed (Fig. 11). The bones of the skull have been disarticulated to a certain extent (Figs. 13, 14), but this is not true for the rest of the skeleton (Fig. 11). As illustrated (Fig. 11) the lower arm has been rotated along its length through 180° because originally the distal half of the humerus lay across the proximal end of the radius and ulna (see Huene, 1906, pls. 2, 3). Some of the bones show evidence of compression because the humerus (Figs. 17A, B), femur (Fig. 21) and the pes (Fig. 22E) are dorsoventrally flattened while the lengths of the vertically held tibia, fibula, astragalus, and calcaneum are unnaturally shortened (Fig. 22B).

SKULL AND LOWER JAW. Both are lightly constructed (Figs. 13, 14) and, prior to preservation, the skull was pushed over laterally (Fig. 13C) and the individual bones were disarticulated to varying degrees (cf. Figs. 13, 14). However, the rami of the lower jaw were preserved in natural articulation with each other and with the quadrates, but the posterior part of the left mandible is no longer preserved (Fig. 13B). As preserved the skull measures 130 mm from tip of the snout to the occipital condyle (Fig. 13B), the right quadrate measures 39 mm, and the right mandibular ramus 110 mm. The large orbits and lateral temporal fenestrae are bordered by slender bones (Figs. 14A, B). The posttemporal fenestra is small (Fig. 14E). There are only a few traces of the nasals (Fig. 13A); so the exact outlines of the narial openings and of the antorbital fenestra are not known but they were probably quite large as reconstructed (Fig. 14A). Judging from the skull of *Plateosaurus* (Fig. 14I), Marsh (1892, 1896; given by Lull, 1915, 1953) was probably incorrect in showing a distinct junction in the dorsal outline between a low snout and a large orbit. However, the anterior half of the skull was probably not as deep as shown by Huene (1906, 1932) and there is no evidence for a deep angulation above the middle of the orbit. The frontals extended over most of the orbit (Figs. 14A, B) and, apart from the more lateral part next to the postorbital, the bone is almost flat anteroposteriorly (Fig. 13A).

The base of the anterior process of the premaxilla (PMX) is stout (Fig. 13A) but this process was probably short (Fig. 14A) as in *Plateosaurus* (Fig. 14I). The left premaxilla of YPM 1883 has two posterior processes (Figs. 13A, 14A), only one of which is preserved on the right side (Fig. 13B). These two processes were lateral to the maxilla (Fig. 14A). In *Plateosaurus* (Fig. 14I) only the dorsal process is present and ventral to this the premaxilla meets the maxilla along a thick and vertical edge. Judging from the size of the one poorly-preserved tooth (Fig. 13B) there were five or six teeth per premaxilla.

The right maxilla (MX) is almost complete and it is low with a short anterior process (Figs. 13A, 14A). The lateral surface is slightly convex

dorsoventrally with an acute edge bordering the antorbital fenestra, the floor of which is formed by an excavation of the main body of the maxilla. The length of the ventral part of the antorbital fenestra is backed by the low medial sheet of the maxilla. In contrast the much higher medial sheet of *Plateosaurus* backs only the anterior half of the antorbital fenestra (Fig. 14I). At the anterior end of the maxilla of YPM 1883 there is a dorsomedial sheet that is preserved at an angle of about 45° to the lateral surface of the bone (Figs. 13A, B). Originally this sheet was probably more horizontal so that it contacted the comparable sheet of the opposite maxilla. Such a median suture between the maxillae is present in *Plateosaurus* (AMNH 6810) and it served to strengthen the snout. The posterior part of the maxilla of YPM 1883 apparently had thin sheets lateral (Fig. 13B) and medial (posterior end of medial sheet, Fig. 13A) to the jugal. The complete series of maxillary teeth is not preserved but, to judge from those preserved, there were probably about nine teeth in each maxilla. The teeth of the maxilla are so poorly preserved that even their shape is uncertain (Figs. 13A, B, 14A).

The nasals (N) are represented by only a few fragments (Fig. 13A) and the outline as restored (Figs. 14A, B) is based on the form of the adjacent bones and the snout of *Plateosaurus* (Figs. 14I, J).

The frontals (F) are thin (Fig. 14A) and somewhat constricted so that much of the orbits are visible in dorsal view (Fig. 14B). Most of the dorsal surface (Figs. 13A, 14A) is very slightly convex transversely and this curvature is most marked in the area adjacent to the postorbital (Fig. 14E). The slender anterior process has a narrow bevel (Fig. 13A) that was overlapped by the prefrontal (Fig. 14B). The posterior process is broader with a depression along its posterior border (Fig. 13A) onto which the dorsal process of the postorbital fitted (Fig. 14B). Proximally this depression occupies about half the width of the process but more distally it tapers to a point. There is a ledge on the more medial part of the frontal which was overlapped by the parietal. The frontals of *Plateosaurus* (Figs. 14I, J) are thicker and broader and are almost completely eliminated from the orbital border by the enlarged prefrontals.

The parietals (P) are separate (Fig. 13A) and were slightly displaced relative to each other during preservation. The lack of union of the parietals may be a primitive feature or it may indicate that YPM 1883 was a young or subadult individual. In *Plateosaurus* some large individuals show traces of the parietal suture (Huene, 1926, 1932), but AMNH 6810 does not. In YPM 1883 each parietal is twisted along its length (Figs. 13A, 14A, B), so that anteriorly the bone is almost horizontal while posteriorly it is at an angle of about 45° with the outer surface facing anterolaterally (Figs. 13A, 14B). Transversely the outer surface is slightly convex anteriorly and gently concave posteriorly. The free medial edge is sharp.
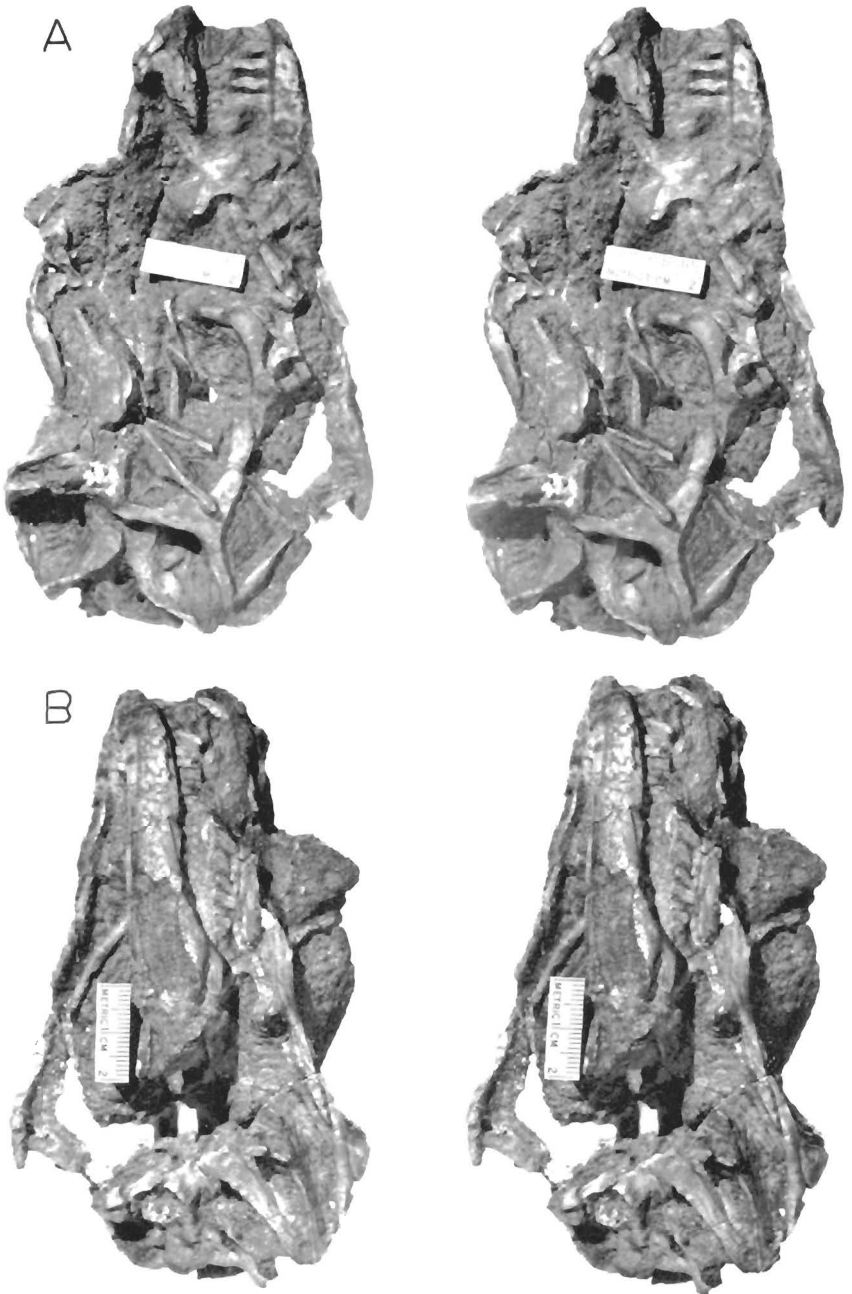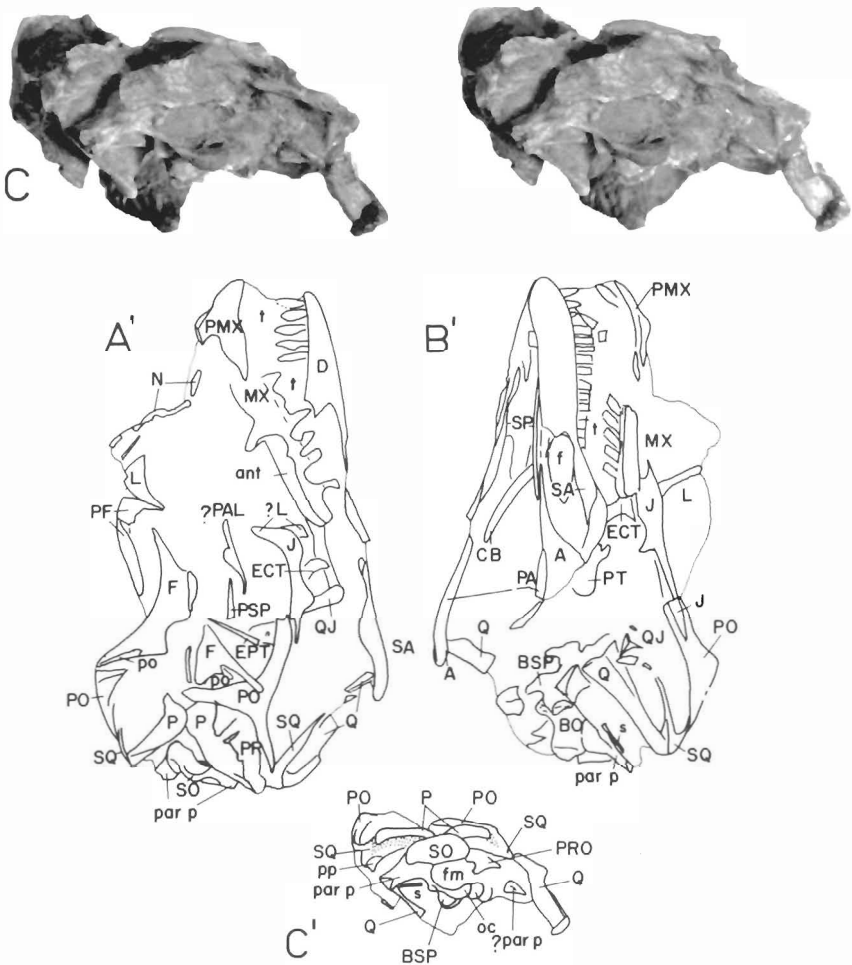
FIG. 13. *Anchisaurus polyzelus*. YPM 1883. Stereophotographs (*A-C*) and explanatory outline drawings (*A'-C'*) of the skull. *A*, laterodorsal view of right side; *B*, ventrolateral view of left side; *C*, posterior view. Abbreviations for Figs. 13-14: *A* = angular: *BO* = basioccipital; *BSP* = basisphenoid; *CB* = first right ceratobrachial; *D* = dentary; *ECT* = ectopterygoid; *EPT* = epipterygoid; *F* = frontal; *J* = jugal; *L* = lacrimal; *MX* = maxilla; *N* = nasal; *P* = parietal; *PA* = prearticular; *PAL* = palatine; *PF* = prefrontal; *PMX* = premaxilla; *PO* = postorbital; *PRO* = prootic; *PSP* = parasphenoid; *PT* = pterygoid; *Q* = quadrate; *QJ* = quadratojugal; *SA* = surangular; *SO* = supraoccipital; *SP* = splenial; *SQ* = squamosal; *ant* = antorbital fenestra; *bpt p* = basipterygoid process; *f* = fenestra; *fm* = foramen magnum; *oc* = occipital condyle; *par p* = paroccipital process; *pp* = surface for paroccipital process; *po* = surface for postorbital; *po f* = posterior fenestra; *s* = stapes; *t* = teeth.
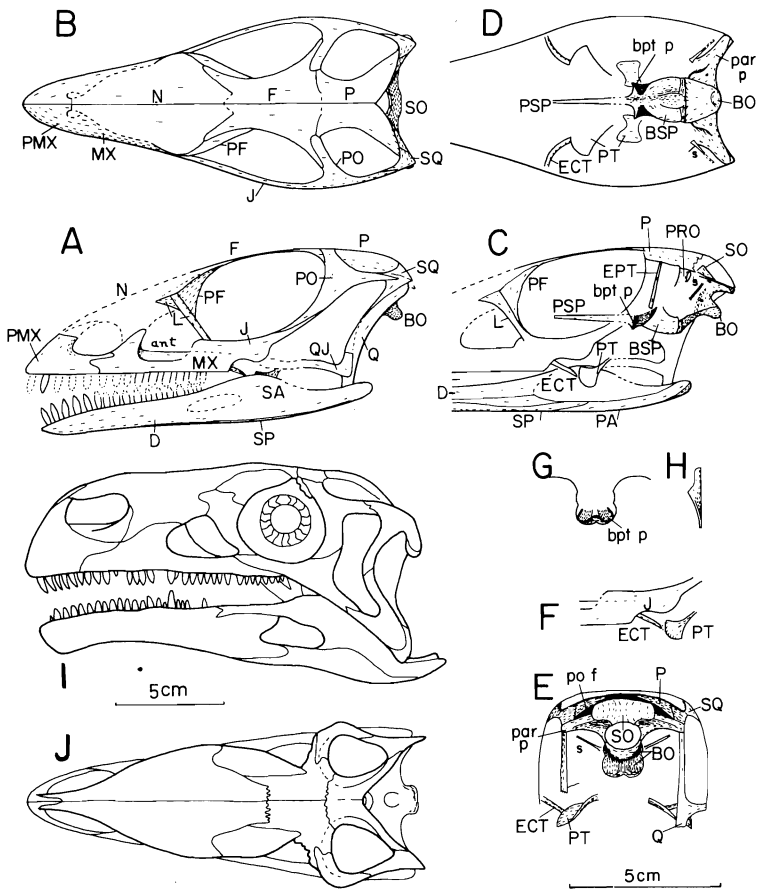
FIG. 14. *A–H Anchisaurus polyzelus.* YPM 1883. Reconstruction of the skull ×
0.4. *A*, lateral view; *B*, dorsal view; *C*, lateral view of braincase and inside view
of right side; *D*, ventral view; *E*, posterior view; *F*, left ectopterygoid and
pterygoid in lateral view; *G*, basipterygoid processes in anterior view; *H*, pos-
sible right palatine; *I, J, Plateosaurus* skull, after Romer (1966) and SMNS
13200. *I*, lateral view; *J*, dorsal view. For abbreviations see Figure 13.

The lacrimal (L) is a slender rod separating the antorbital fenestra from the orbit (Figs. 13B, 14A). The ventral end is slightly expanded and it fitted against the medial surface of the maxilla (and possibly the jugal). The dorsal end has a slight anterior expansion that was slightly overlapped by the nasal. The prefrontal fitted against the dorsal part of the posterior edge.

The roughly L-shaped prefrontal (PF) is twisted so that the broader anteroventral part faces laterally (Figs. 13A, 14A) while the tapering posterodorsal part faces dorsally (Figs. 13A, 14B). The latter part slightly overlapped the frontal and formed the anterodorsal margin of the orbit (Fig. 14B). In *Plateosaurus* (Figs. 14I, J) this part is much longer and broader.

Lull (1915, 1953) mentioned postfrontals and indications of them were shown (Lull, 1953, fig. 15B from Marsh, 1892, 1896; see also Huene, 1906, fig. 1, pl. 1). However, this identification is based on the presence of a "suture" which is actually a break (complete with plaster and glue) across the left frontal. There is no corresponding "suture" on the right frontal so the "postfrontal" is the lateral part of the frontal. Huene (1926, pl. 1, figs. 1, 2) indicated postfrontals in *Plateosaurus*, but an examination of the specimen (SMNS 13200) shows that on both sides the suture between the postfrontal and the postorbital is a break across the postorbital. There is no sign of such a suture in AMNH 6810 or in some of the skulls figured by Huene (1932). This region is correctly shown by Romer (1966; see Figs. 14I, J this paper).

The three processes of the postorbital (PO) are of unequal length (Figs. 13A, 14A, B) and have sharp edges. The short posterior process is triangular in cross section and overlapped the squamosal (Fig. 14A). The broad and thick medial process overlapped the frontal (Figs. 13A, 14B). The jugal fitted onto a groove on the posterior surface of the much thickened and elongate ventral process (Figs. 13B, 14A).

Both jugals (J) are slightly incomplete (Figs. 13A, B, 14A) and the left appears to be in natural association with the surrounding bones. There is a long overlapping suture between the slender and tapering posterodorsal process and the postorbital (Fig. 13B, 14A). The resulting bar is much stronger than it looks in lateral view (Fig. 14A) because the thickness is greater than the width. The exact outline of the more ventral part of the jugal adjacent to the quadratojugal is uncertain. The step between the dorsal edge of the jugal and the maxilla may be natural (Fig. 13B, 14A).

The squamosals (SQ) are complete and each is a tetraradiate bone with rather unequally developed processes (Figs. 13A, B; 14A, B). The short, slender and tapering anterior process is overlapped by the postorbital (Fig. 14A). The longer and broader medial process overlaps the parietal (Figs. 14A, B) and the distal part of the paroccipital process (Fig. 14E). The very long and tapering ventral process is triangular in section and borders the

dorsal part of the quadrate (Figs. 13A, B; 14A). The tip of the stout but very short posterior process (Fig. 14A) was probably the point of origin of the M. abductor mandibulae. A thin sheet connects the medial part of the posterior process to the medial part of the dorsal half of the ventral process, the more lateral part of which forms a comparable but smaller sheet. These two sheets and the ventral surface of the posterior process form a socket into which fitted the dorsal head of the quadrate (Fig. 14A). The dorso-lateral surface of the body of the squamosal is gently convex antero-posteriorly and transversely. The lateral surface of the ventral process is at an angle of about 120° to it. These two surfaces are separated by a ridge which is emphasized by an excavation ventral to it (Figs. 13B, 14A). This ridge probably marked the dorsal limit of the M. adductor externus super-ficialis as does a similar ridge in ornithopods (Ostrom, 1961; Galton, 1974).

The right quadratojugal (QJ) is very incomplete and it is preserved next to the quadrate (Fig. 13B). A thin L-shaped element on the left side in close proximity to the jugal and the maxilla appears to be the displaced left quadratojugal (Figs. 13A, 14A). In *Plateosaurus* the quadratojugal is Y-shaped (Fig. 14I) and the difference in shape appears to be correlated with the orientation of the ventral part of the quadrate: slightly anteriorly in *Anchisaurus* as against slightly posteriorly in *Plateosaurus* (Figs. 14A, I).

The median vomers are not visible because they are hidden by the maxillae and the mandibular rami (Fig. 13). Part of one of the palatines (PAL) may be represented by a single asymetrical bone that is visible on the right side of the block (Figs. 13A, 14H). The bone is thin, twisted along its length and is incomplete ? anteriorly.

The ectopterygoid (ECT) is a slender and slightly curved and twisted bone (Figs. 13B, 14C-F). The sutural area for the jugal is expanded posteriorly whereas that for the pterygoid is not visible.

The left pterygoid (PT) lacks the central part, but it was obviously a large bone. The sectioned alar process for the quadrate is visible close to the medial surface of the quadrate. The broad but thin pterygoid flange is obliquely oriented (Figs. 13B, 14D, E, F) and is twisted so that the medial and distal parts are perpendicular to each other. The dorsal surface of the medial part is concave anteroposteriorly and the lateral surface of the distal part is gently rounded (Fig. 14F).

The right epipterygoid (EPT) is a very slender and tapering rod (Fig. 14C) that during preservation was displaced slightly into the right orbit (Fig. 13A).

Both quadrates (Q) are present (Fig. 13) but during preservation the right was rotated 90° clockwise around its longitudinal axis and the ventral part is missing (Fig. 13A). The lateral surface is flat with a sharp edge posteriorly for most of the length except ventrally where the quadrate thickens to form the mandibular condyle (Figs. 13, 14A, E), the exact form of which cannot be determined. Set at an angle of about 135° to the

lateral surface is the alar process which overlapped the more medial pterygoid. This alar process is widest at its ventral edge (about 10 mm above the mandibular condyle) and tapers to nothing about 5 mm from the top of the bone. For most of its length the angle between the alar process and the lateral surface is marked by a slight ridge. However, more dorsally it is marked by a thin sheet formed by the anterior expansion of the lateral part. In *Plateosaurus* (Fig. 14I) this projecting sheet is very much longer and extends the length of this contact to give a much more robust and stronger quadrate.

The braincase is well exposed in ventral (Figs. 13B, 14D) and posterior views (Figs. 13C, 14E), but only part of the right side-wall is visible (Figs. 13B, 14C) and the right exoccipital and opisthotic are missing. During preservation the floor of the braincase was bent at the basisphenoid-basioccipital suture and, as a result, the anterior part of the braincase is directed dorsally at an angle of about 45° to the basioccipital. The loss of part of the right side-wall, the parting of the suture in the floor and the separate parietals indicate that YPM 1883 was probably a young individual in which the bones surrounding the brain were not as fully coossified as in an adult animal.

The parasphenoid (PSD) is a slender and slightly tapering rod (Figs. 14C, D) which is exposed on the dorsal surface of the block (Fig. 13A). Ventrally at the base there is a median furrow (Fig. 14D) that continues posteriorly onto the basiphenoid (BSP), the anterior part of which is expanded to form the basipterygoid process which articulated with the pterygoids. These processes are very small (Figs. 14C, D) in comparison with those of *Thecodontosaurus* (YPM 2192) and *Plateosaurus* (Huene, 1926). Each process is a thin curved sheet with a concave anterior surface and, because of the symmetry of the two processes, the small size is not the result of erosion or breakage. However, bearing in mind the evidence of immaturity noted above it is possible that the basipterygoid processes were incompletely ossified and that they were continued more distally as cartilage. Posterodorsal to these processes the lateral wall of the basisphenoid is deeply excavated (Fig. 14C). In ventral view (Fig. 14D) the constricted bone widens out more posteriorly to form two basal tubera that are separated by a deep median depression. It should be noted that the part labelled by Marsh (1893, 1896; see Lull, 1953, fig. 15C) as the basipterygoid process is actually one of the basal tubera.

The exposed part of the anterior sutural surface of the basioccipital (BO) consists of two ridged areas separated by a deep embayment (Fig. 14D). The ventral surface is gently concave transversely, concave antero-posteriorly with the curvature becoming progressively more marked towards the midline. The occipital condyle is slightly eroded (Figs. 13B, C) with a small lateral component from each exoccipital (Fig. 14E). There is no suture; so the extent of contribution of the exoccipital and of the opisthotic to the lateral wall of the braincase and to the paroccipital process cannot be determined.

The tip of the paroccipital process (*par p*) is missing and the distal part is triangular in cross section with the three edges continuing more proximally. The sharp anterior edge forms the leading edge of the process, the more rounded posterodorsal edge is overlapped by the ventral corner of the supraoccipital (Figs. 13C, 14E) and the sharp ventral edge was overlapped by the tapering posterodorsal apex of the prootic (visible in medial view on right prootic). More proximally the posteroventral surface is subdivided by a secondary ridge which extends ventromedially to the occipital condyle (Figs. 13C, 14E). The surface dorsal to this ridge is dorsoventrally concave and borders the foramen magnum more medially (Figs. 13C, 14E). The concave surface ventral to the secondary ridge is subdivided by a fold (Fig. 14D) which extends anteroventrally towards the basal tubera (Fig. 14C). The posterior border of this fold is perforated by two foramina (Fig. 13B), both of which may have been for the hypoglossal nerve (XII) as Huene (1906) suggested. However, the smaller more ventrally situated foramen may have been for the accessory nerve (XI). The area anterior to the fold is hidden by matrix with the stapes preserved *in situ* (Figs. 13B, C; 14D, E). Into this anterior area would have opened the foramen lacerum (for cranial nerves IX, X, XI), the foramen jugulare (for the internal jugular vein) and the fenestra ovalis which was probably bordered anteriorly by the prootic (PRO), part of the gently curved lateral surface of which is visible on the right side (Figs. 13A, 14C).

The supraoccipital (SO) is a subrectangular bone, the lateral parts of which are flat while the medial part is transversely convex (Figs. 13C, 14E). The amount of medial curvature progressively increases passing dorsally so that about two-thirds of the dorsal edge forms almost a semicircle (Fig. 13A). The supraoccipital is extensively overlapped by the parietal (Figs. 13A, 14B) and itself overlaps the paroccipital process more laterally (Figs. 13A, C; 14E).

The only part of the lower jaw no longer preserved is the posterior part of the left ramus. Each mandibular ramus is slender with a low coronoid elevation (Figs. 13A, B, 14A) which is not as large as shown by Marsh (1892, 1896; in Lull, 1953) and Huene (1906, 1932). As indicated by Huene (1906, 1932) there are traces of a mandibular foramen (Figs. 13B, 14A) but its posterior outline is difficult to determine because this area is somewhat worn. Each dentary (D) is low and slender, the anterior symphysis was not coossified and much of the ventral edge is sharp. The anterior dentary teeth are slender and slightly recurved, the middle teeth are broader and the posterior ones smaller but the exact form of most of the teeth is indeterminate (Fig. 14A). There are 15 teeth preserved *in situ* in the left dentary and the full count was probably 16 (Figs. 13B, 14A). The posterior part of the lower jaw is not well preserved (Figs. 13A, B) but it appears to have been like that of *Plateosaurus* (Fig. 14I). Very little of the lower jaw is visible in medial view (Figs. 13B, 14C). The splenial

(SP) is a thin and slender element which covered the Meckelian canal and formed a small part of the ventral edge of the lower jaw (Fig. 14A). The slender prearticular (PA, Figs. 13B, 14C) forms the posteroventral part of the lower jaw.

ACCESSORY ELEMENTS. The stapes (s, Figs, 13B, C, 14C–E) is a very slender rod with a slightly expanded proximal end which in life fitted against the fenestra ovalis. Distally the stapes would have attached to the tympanic membrane, the dorsal margin of which was supported by the ventral edge of the paroccipital process. There is no trace of sclerotic plates but these were probably present as in most other sauropsids including *Plateosaurus* (Huene, 1926). The hyoid apparatus is represented by the right first ceratobrachial (CB, Fig. 13B), a slender and slightly S-shaped rod, oval in cross section with sharp edges.

VERTEBRAL COLUMN. The articulated column includes the first three cervical vertebrae, the complete dorsal series and the first two sacral vertebrae. The atlas is represented by the right neural arch plus the longitudinally sectioned intercentrum (Figs. 15A, B). The medial surface of the neural arch is concave dorsoventrally with the degree of curvature progressively increasing more anteriorly (Fig. 15A). The prezygapophysis is a thickening of the anterodorsal part of the neural arch. The surface lateral to the post-zygapophysis is concave anteroposteriorly (Fig. 15B).

The axis (Figs. 15C, D) is low and similar to that of *Plateosaurus* (Huene, 1926; AMNH 6810) except that the neural spine is longer and extends onto the anterior part of the postzygapophyses. As a result of this the posterior part of the neural spine roofs a space that is partly floored by the broad postzygapophyses. Anteriorly the dorsal edge of the neural spine thickens and terminates as a projecting point (Fig. 15D). The prezygapophysis is represented by a slight ridge on the anteroventral part of the neural arch (Figs. 15C, D). The neurocentral suture is plainly visible (Fig. 15D), but the anterior and posterior parts of the centrum are damaged. Fragments of the slender rib are preserved on the left side of the axis (Fig. 15D).

Relative to the axis and in its proportions (Fig. 15F) the third cervical vertebra is more elongated than that of *Plateosaurus* but, apart from this, it is very similar (more so to AMNH 6810 than to UT 2). The neural spine is low and anteriorly it forms an anteroventrally directed projection. The diaphysis is small, projecting only slightly laterally (Fig. 15E), but the region of the paraphysis is obscured by matrix. The sides of the centrum are constricted transversely and the ventral edge is sharp. Although only the bases of the postzygapophyses are preserved there are indications of the posteroventral limit of the centrum (Fig. 15F).
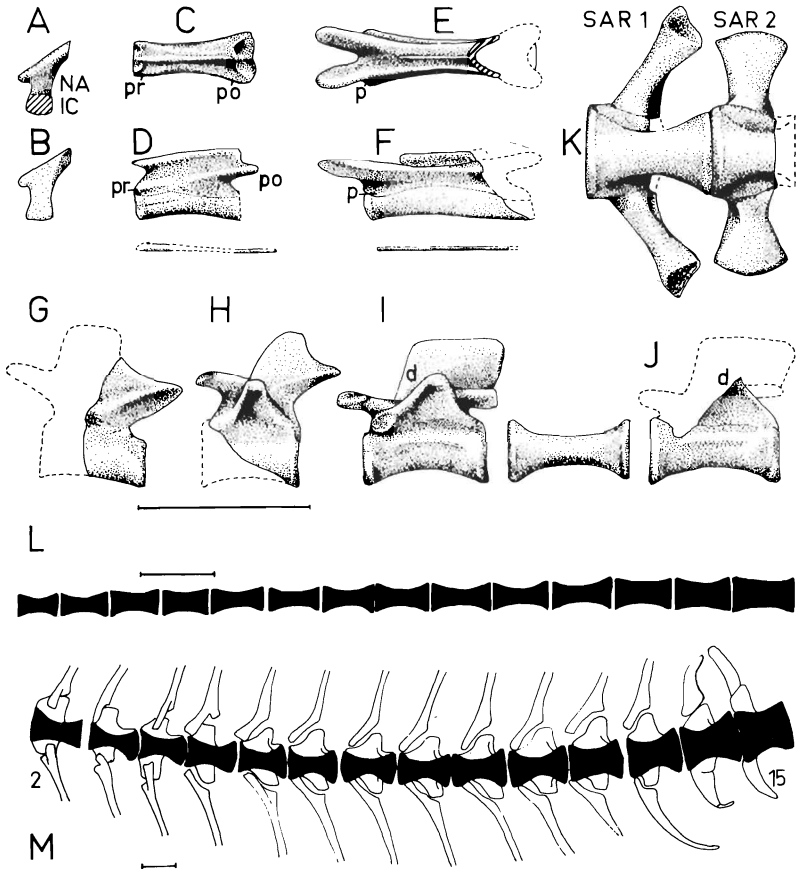
FIG. 15. *Anchisaurus polyzelus*. YPM 1883. Vertebrae × 0.45. *A–F*, Cervical vertebrae: *A*, right neural arch of atlas in medial view; *B*, atlas in lateral view; *C*, axis in dorsal view; *D*, axis with rib in lateral view; *E*, cervical vertebra 3 in dorsal view; *F*, cervical vertebra 3 with rib in lateral view. *G–J*, Dorsal vertebra in lateral view; *G*, posterior part of dorsal vertebra 1; *H*, dorsal vertebra 2; *I*, dorsal vertebra 10 with ventral view of centrum; *J*, dorsal vertebrae 12; *K*, sacral vertebrae 1 and 2 with ribs in ventral view; *L*, dorsal vertebrae 2 to 15 in ventral view; *M*, as *L* for *Plateosaurus*, from a photograph of UT1. Abbreviations: *IC* = intercentrum: *NA* = neural arch; *SAR* 1 and 2 = sacral ribs 1 and 2; *d* = diaphysis; *po* = postzygapophysis; *pr* = prezygapophysis. Horizontal lines represent 5 cm.

DORSAL VERTEBRAE AND RIBS. If it is assumed that there were 15 dorsal vertebrae in YPM 1883 as is the case in *Efraasia* (Galton, 1973a) and *Plateosaurus* (Huene, 1926) then the complete series is preserved on the main block (Figs. 11, 15E–L). In most cases only the centra are visible (for measurements see Table 2) but those of the fourth and fourteenth dorsals are covered by the right coracoid and the pubes respectively (Figs. 11, 12). The first dorsal vertebra is very incomplete (Fig. 15G) and the second is damaged, but the centrum was obviously short (Fig. 15H). The third centrum has an acute median edge (Fig. 11) and the fifth centrum also has a sharp ventral edge, but because it is asymetrically situated on the right side, this edge is undoubtedly an artifact of preservation. The ventral surfaces of the remaining centra until the thirteenth are gently convex transversely and the gently rounded longitudinal edges are sub-parallel, but towards each end the centra flare out markedly (Figs. 11, 12, 15L) and, as a result of this, the anterior and posterior edges of the centra are acute. A section through the anterior part of the centrum of the eighth dorsal vertebra (Fig. 11, centrum *DOR 8*) shows that the end surface was strongly concave; so presumably the centra were markedly amphycoelous as is the case in *Ammosaurus* (UCMP 82961). The central parts of the centra are pinched in slightly transversely to form a slight pleurocoel on each side (Figs. 15I, J). In lateral view (Figs. 15I, J) the centra appear to be elongate in comparison with those of *Plateosaurus,* but there is much less difference in ventral view (Figs. 15L, M). The hind limb to trunk ratio is about 0.90 in *Anchisaurus* as against 0.98 for *Plateosaurus,* but in the latter the height of a middorsal centrum is about 75% of its length whereas in *Anchisaurus* it is only 45%. The proportionally greater depth of the centrum of *Plateosaurus* is an adaptation for greater size and similar differences can be seen between small and large genera of ornithopod dinosaurs. The centrum of the fifteenth dorsal is long and massive with a gently convex ventral surface (Fig. 12).

The left transverse process of the second dorsal vertebra is buttressed ventrally by two transverse laminae (Fig. 15H) that are also well developed on dorsals 3, 8 and 12, the only other dorsals in which this region is visible. The neural spine of the second dorsal is short anteroposteriorly and thin (Fig. 15H), but that of dorsal 9 (Fig. 15I) is much more elongate as are those of dorsals 13 and 14 in which the outline is very similar. The post-zygapophysis of dorsal vertebra 9 (Fig. 15I) has a zygosphene articulation; the ventral part of the articular surface is vertical and oriented antero-posteriorly (Fig. 15I, cf. Fig. 4). Unfortunately it is not possible to further prepare the dorsal series to expose the dorsal and lateral surfaces of the neural arches.

The dorsal ribs have been flattened in preservation but most of them are well displayed on the main block (Fig. 11). Dorsal ribs 6 to 12 on the left side and ribs 4 to 6 and 13 of the right side are complete and in natural

articulation. The lengths of the ribs measured along the curve to the tuberculum are given in Table 2. The capitulum is visible on ribs 8 and 11 and in both it is well separated from the tuberculum.

SACRUM. The first two sacral vertebrae are exposed in ventral view with the ribs of the right side in articulation, but the incomplete second sacral was displaced during preservation (Figs. 12, 15K). The centrum of the first sacral is massive and the ventral surface is gently convex, as is that of the much smaller second centrum. The first sacral rib is elongate with expanded ends. Proximally the ventral surface is flat with an acute edge posteriorly. The rest of the ventral surface is gently convex anteroposteriorly and gently concave transversely. The distal end has a subtriangular and rough surface that presumably fitted against the base of the pubic peduncle of the ilium as in *Ammosaurus* (Fig. 26). The second sacral rib of YPM 1883 is shorter but broader with most of the ventral surface flat. Proximally part of the bone is transversely concave and the anterior part is excavated to form a diagonally inclined and sharp edge that merges more distally. A comparison of the first two sacral ribs with the medial surface of the ilium (Fig. 19C) indicates that the sutural surface posterior to the ischiadic head was probably for a third sacral rib.

PECTORAL GIRDLE AND FORELIMB. During preservation the pectoral girdle was displaced against the vertebral column (Fig. 11). The left coracoid is the most complete (Fig. 16A), but the anterior part is missing and the exact form of the ventral outline cannot be determined (cf. Fig. 16C). Laterally immediately below the glenoid cavity there is a prominent horizontal ridge that shortly merges with the lateral surface (Figs. 16A, C). There is no sign of the coracoid foramen, but the surface of the relevant areas is damaged.

Only two-thirds of the left scapula is preserved as bone (Fig. 11), but much of the rest of the outline is represented by a natural mold of the ventral surface (Fig. 16A). The right scapula is preserved at an acute angle to the coracoid so that the medial surface of both ends is visible (Fig. 11) and further preparation revealed much of the other side (Fig. 16C). Most of the lateral surface is gently convex transversely and longitudinally, but the anteroventral part of the broad proximal end is excavated to form a prominent depression (Figs. 16A, C). Consequently the anteroventral part is very thin whereas the region dorsal to the glenoid cavity is very thick (Fig. 16B). The nature of the surface of the glenoid cavity cannot be determined. The shaft is very slender, oval in cross section with sharp edges and it is slightly twisted so that the relatively unexpanded blade region is at an angle of about 40° to the broad proximal part.
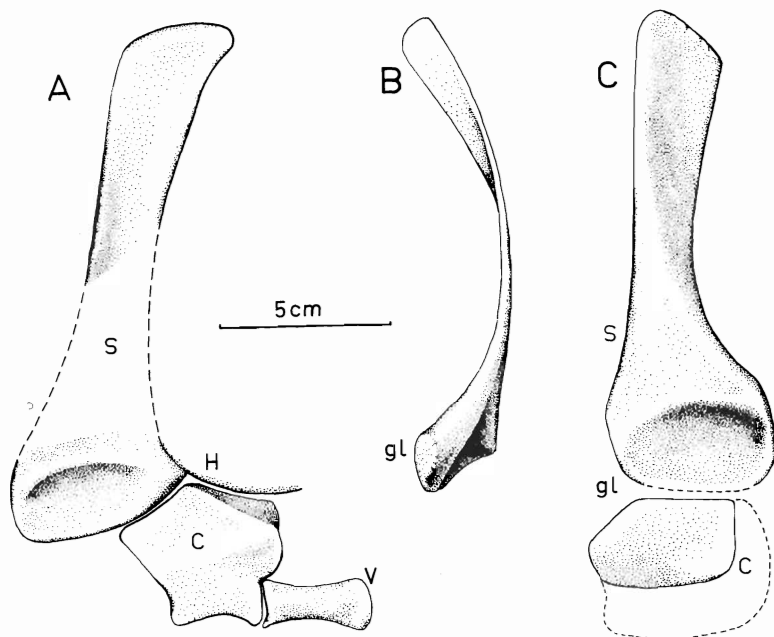
FIG. 16. *Anchisaurus polyzelus.* YPM 1883. Scapula and coracoid × 0.45. *A*, left scapula and coracoid in lateral view, scapula has been straightened out; *B*, right scapula in posterior view; *C*, right scapula and coracoid in lateral view. Abbreviations: *C* = coracoid, *H* = overlying humerus; *S* = scapula; *V* = centrum of dorsal vertebra 4; *gl* = glenoid cavity.

Only the proximal part of the left humerus is preserved (Fig. 11) but the right forelimb is complete except for a few phalanges (Figs. 11, 17, 18). Originally the distal half of the humerus was on top of the radius and ulna with the elbow flexed at an angle of about 45° (see Huene, 1906, pls. 2, 3). All three bones are artificially flattened; this is especially true for the distal part of the humerus (Figs. 17A, B) and the middle part of the ulna (Figs. 17C, 18). The proximal end of the ulna is rough textured and the short horizontal ridge (Figs. 17C, 18) on the proximal part is natural. The cross section of the radius is oval for much of its length, but originally it was probably circular.

The manus (Figs. 17C, 18) is typically prosauropod in form with a large first distal carpal (displaced laterally during preservation), a massive first digit, subequal second and third digits and reduced lateral digits. Metacarpal 1 is short and robust and the proximal end is subtriangular in outline with a gently concave lateral surface for metacarpal 2. The distal ginglymus is asymetrical as in *Ammosaurus* (Figs. 36A–D) and *Plateosaurus* (UT1) so
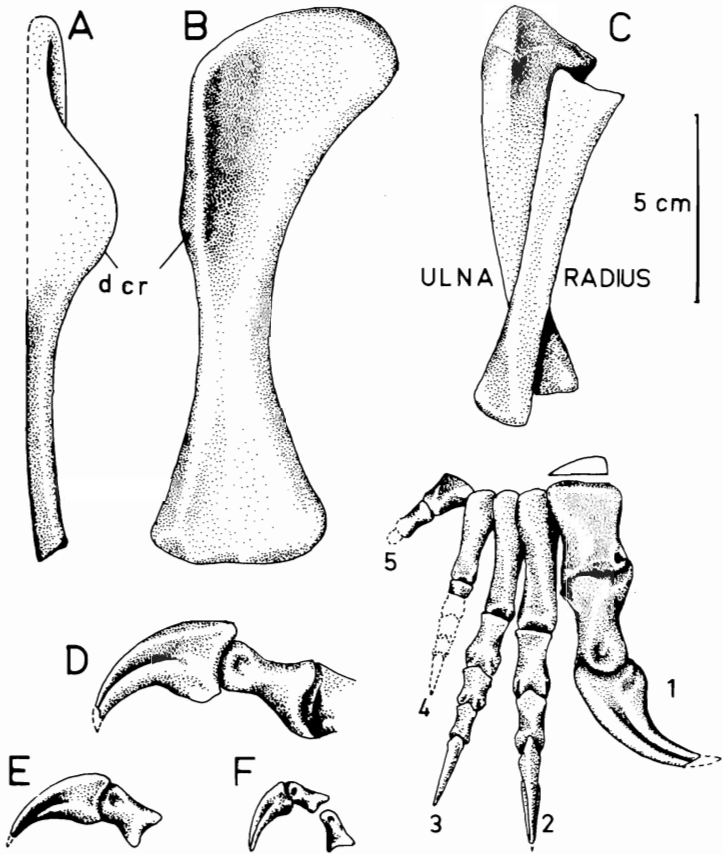
FIG. 17. *Anchisaurus polyzelus.* YPM 1883. Right forelimb × 0.5. *A*, humerus in lateral view; *B*, humerus in anterior view; *C*, forearm and manus in lateral view; *D–F*, dorsal view of distal phalanges of digits 1, 2 and 3 (*D, E, F*). Abbreviations: *d cr* = deltopectoral crest; 1–5, digits 1–5.

that during flexion the ungual phalanx would have rotated laterally to line up with the other digits (Galton, 1971b). The first phalanx is slightly compressed (Figs. 17C, 18) but originally it was very like that of *Ammosaurus* (Figs. 36F–K) and *Plateosaurus*. In particular the medial concavity of the proximal end is the largest and the phalanx is twisted so that the plane of articulation of the proximal and distal condyles are at an angle of about 45° to each other (this angle is exaggerated by a slight amount of crushing in YPM 1883). The first ungual phalanx (Figs. 17C, D, 18)
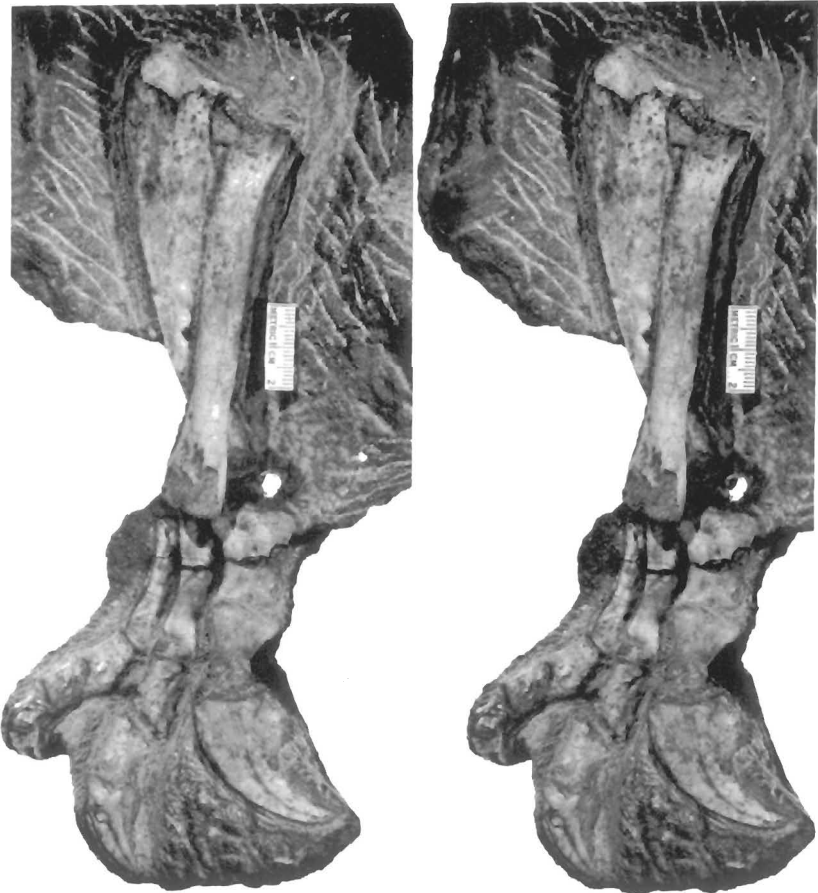
FIG. 18. *Anchisaurus polyzelus*. YPM 1883. Stereophotograph of right forearm and manus; compare with Figure 17C.

has a very prominent ventral process for flexor tendons and a prominent claw groove. This phalanx is somewhat less trenchant than that of AM 41.109 (Fig. 7I), but as in AM 41/109 metacarpals 2 to 5 are very slender (Figs. 7A, L, 17C, 18), a condition matched only by the material referred to *Thecodontosaurus* and *Efraasia* (Galton, 1973a). The phalanges of digits 2 and 3 are slender (Figs. 17C, 18) and the ungual phalanges differ from that of digit 1 in being much smaller, less trenchant and in lacking a prominent flexor process ventrally (Figs. 17C-F).

PELVIC GIRDLE AND HIND LIMB. The apronlike region of the left pubis plus
the pubis, ilium, and part of the ischium of the right side (Fig. 19) are
preserved (Fig. 12). The ilium is slightly displaced and the dorsal part
is crushed over medially. Originally the lateral surface was longitudinally
concave and the ilium (Fig. 19A) is very similar to that of *Ammosaurus*
(Fig. 26E) in having a long anterior process. In all other prosauropods
except *Anchisaurus capensis* (Broom, 1911; Galton and Cluver, in press)
the anterior process is a small triangle. The ventral edge of the anterior
process of YPM 1883 becomes progressively thicker more posteriorly. The
large pubic peduncle is subtriangular in cross section with a gently convex
dorsal surface (Figs. 19A, C), a gently concave acetabular surface (Fig. 19B)
and a flat medial surface (Fig. 19C). Most of the lateral part of the broad
acetabulum is thin with a sharp edge. The end of the pubic peduncle
(Fig. 19B) and the ischial head (Figs. 19A–C) are covered by porous bone
which in life was probably covered with cartilage. The exposed part of the
medial surface (Fig. 19C) is flat with a rugose area above the ischial
head for the anterior part of the third sacral rib (p. 38).

The reconstruction of the pubis (Figs. 19, 20A–C) is best understood
by comparing it with the more usual form for a prosauropod as shown by
Efraasia (Figs. 20D–F) and *Ammosaurus* (Figs. 26E, F). In *Efraasia* the
deep subacetabular region is set at an angle of about 45° to the vertical and
it is perforated by an obturator foramen (Figs. 20D, E). The subacetabular
region is connected by a twisted region to the broad and horizontal apron-
like distal part of the pubis (Figs. 20D, E). The bone adjacent to the fora-
men is very thin and is indicated by the more deeply shaded area (Fig.
20E). The pubis of *Anchisaurus* does not appear to be twisted, but this
is a result of the loss of the thin bone from the subacetabular region
(Figs. 20A, E; 20C, D). The obturator foramen is very large and lacks a
ventral border. The part of the pubis adjacent to the ischium tapers ventrally
to a point (Figs. 19A, 20A, C) and further preparation established that this
is natural. The acetabular surface is concave both longitudinally and
transversely with a sharp lateral edge. Proportionally the width of the
horizontally held distal part of the pubis (Fig. 12) has been reduced so that
this part is more rod-like than in other prosauropods (cf. Figs. 20C, D).
The pubic rods are suboval in cross section with the greatest thickness in
the lateral third. The lateral and especially the medial edges are sharp. The
proximal part of the right pubic rod was rather shattered and distorted
during preservation (Fig. 12). The distal end is expanded dorsoventrally
with a rough-textured and gently convex surface (Fig. 20B). A small piece
of the pubic rod would be quite similar to the isolated piece of AM 41/109
(Fig. 6K).

Only a small portion of the proximal end of the right ischium is pre-
served (Figs. 12, 19A). The acetabulum occupies about half of the width
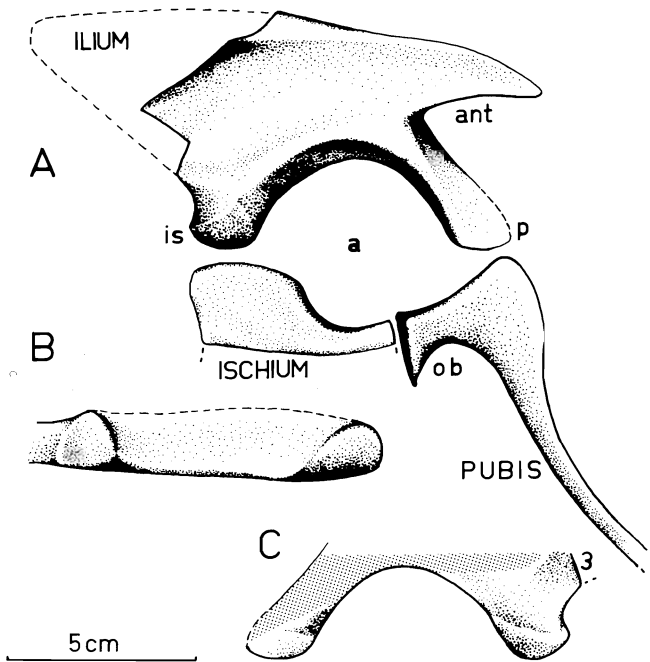with the rest forming a large head for the ilium. Unfortunately it cannot

FIG. 19. *Anchisaurus polyzelus.* YPM 1883. Pelvic girdle × 0.5. *A*, right pelvic girdle in lateral view; *B*, right ilium in acetabular view; *C*, right ilium in medial view. Abbreviations: *a* = acetabulum, *ant* = anterior process; *is* = surface for ischium; *ob* = open obturator foramen; *p* = surface for pubis; *3* = surface for sacral rib 3.

be established whether or not the ischium showed a ventral emargination comparable to that of the pubis (Fig. 19A).

Although the femur is somewhat crushed dorsoventrally (Figs. 12, 21) it is almost identical to that of AM 41/109 (Fig. 8). Comparisons show that only part of the head is missing (Fig. 21) and the proportionally smaller fourth trochanter of AM 41/109 shows signs of erosion. The lesser trochanter is a sharp and well-defined ridge that merges with the surface more dorsally (Figs. 21A, B) as in AM 41/109 (Figs. 8A, D). The dorsal part of the trochanter does not project freely to form a process more dorsally as shown by Marsh (1892, 1893, 1896; in Lull, 1915, 1953). Marsh's figures are also incorrect in showing a prominent anterior intercondylar groove at the distal end of the femur. Further preparation shows that this region resembles that of AM 41/109 (Figs. 8D, I) in having only the slightest trace of a groove. Posteriorly (Fig. 21C) the outer condyle is much more plate-like than the massive inner condyle and
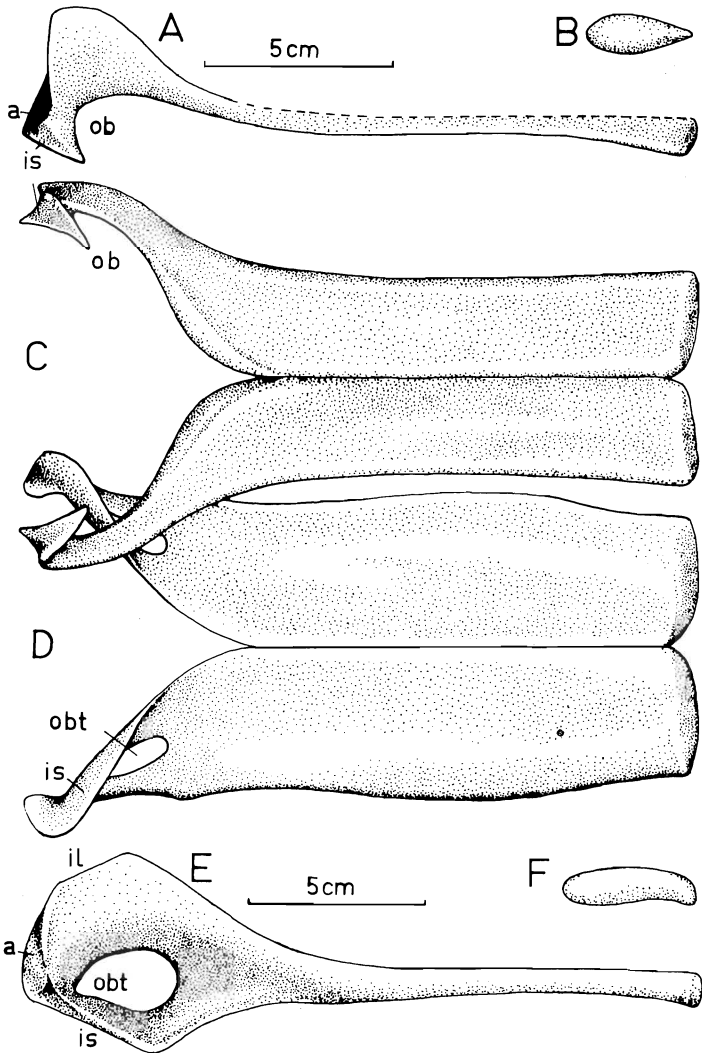
FIG. 20. *Anchisaurus polyzelus.* YPM 1883. Pubes × 0.5. *A*, right pubis in lateral view; *B*, distal end of right pubis; *C*, pubes in anterodorsal view; *Efraasia diagnostica*, SMNS 12667, slightly less than × 0.5. *D*, pubes in anterodorsal view; *E*, right pubis in lateral view; *F*, distal end of right pubis. Abbreviations: *a* = acetabulum; *il* = surface for ilium; *is* = surface for ischium; *ob* = open obturator foramen; *obt* = obturator foramen.
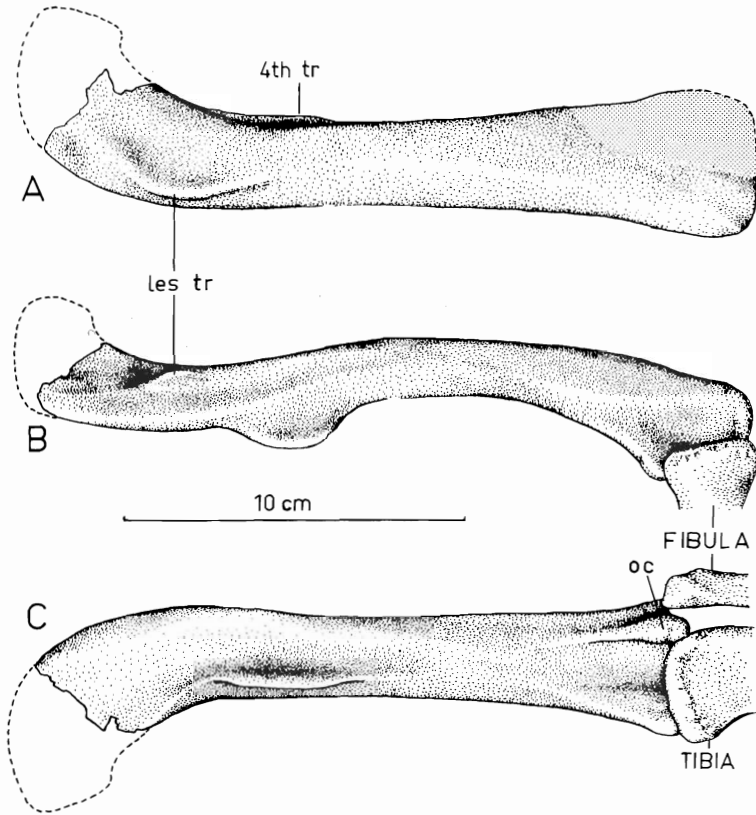
FIG. 21 *Anchisaurus polyzelus.* YPM 1883. Right femur × 0.45. *A*, dorsal view: *B*, lateral view; *C*, ventral view. Abbreviations: *les tr* = lesser trochanter; *oc* = outer condyle; *4th tr* = fourth trochanter.
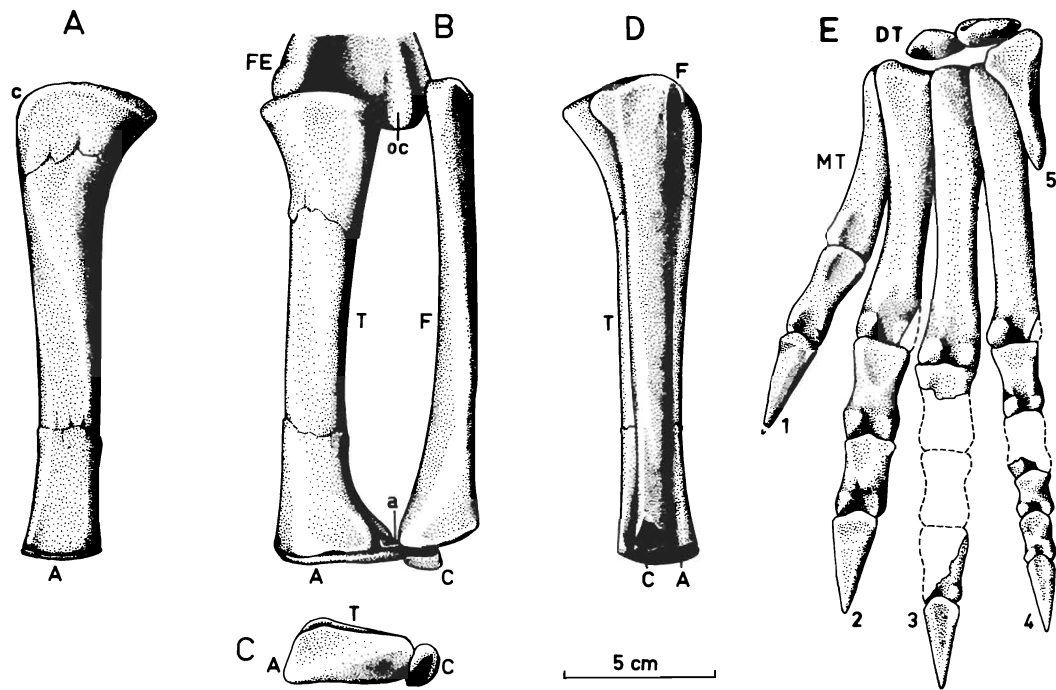
FIG. 22. *Anchisaurus polyzelus*. YPM 1883. Right lower leg and pes × 0.4. *A*, tibia in medial view; *B*, tibia and fibula in posterior view; *C*, astragalus and calcaneum in distal view; *D*, tibia and fibula in lateral view; *E*, pes in ventral view; compare with Figure 12. Matrix indicated by mechanical shading. Abbreviations: *A* = astragalus; *C* = calcaneum; *DT* = distal tarsals; *F* = fibula; *FE* = femur; *MT* = metatarsus; *T* = tibia; *a* = ascending central process of astragalus; *c* = cnemial crest; *oc* = outer condyle.

becomes sharp-edged more proximally. The distal parts of these condyles are hidden by the tibia and fibula (Figs. 21B, C).

The tibia and fibula are very short in comparison with the femur (Figs. 21, 22), but this is probably unnatural. During preservation compressive forces clearly flattened the horizontally held humerus, ulna, femur, and pes (Fig. 11). The vertically held tibia and fibula show evidence of crushing and telescoping; the astragalus and calcaneum have been flattened to form thin, capping sheets (Fig. 22C). The tibia and fibula have been straightened but no compensation has been made for the shortening (Figs. 22A, B, D). The proximal end of the tibia is similar to that of AM 41/109 (Figs. 9A–D). One difference is that YPM 1883 is broader in posterior view (Fig. 22C), because the compressive forces during preservation were vertical to the tibia rather than transverse as in AM 41/109 (Figs. 9D, E). All surfaces are gently convex but near the distal end the lateral surface becomes concave with a thin and sharp-edged sheet both anteriorly and posteriorly (Fig. 22B). The resulting depression for the fibula is short as in *Efraasia* (Galton, 1973a), whereas in *Ammosaurus* is it much longer (Fig. 27A).

The fibula has an expanded proximal end (Fig. 22D) with a flat medial surface and a lateral surface which is gently concave longitudinally and gently convex transversely. The anterior edge is more acute than the posterior edge; both edges become rounded more distally so that the middle of the shaft is circular in cross section. The distal part is expanded transversely (Fig. 22B) but the extent of this was somewhat exaggerated during preservation. The distal end is slightly oval in outline with a gently convex surface.

The astragalus (Figs. 22A–C) is considerably compressed to form a thin, capping plate that is probably only about a third of its original thickness. The ventral surface (Figs. 11, 22C) is gently convex anteroposteriorly; transversely the central part is gently concave and the rest is gently convex. The central ascending process of the astragalus keys into the lateral part of the tibia (Fig. 22D). The calcaneum is also much flattened and it is very small (Fig. 22B–D). The exposed ventral surfaces of the two distal tarsals are gently convex (Figs. 11, 22E).

The pes has been flattened dorsoventrally, but despite this the metatarsals and phalanges are remarkably slender (Figs. 11, 22E) as in AM 41/109 (Fig. 10B, I,), *Anchisaurus capensis* (Galton and Cluver, in press), *Efraasia* and the specimens referred to *Thecodontosaurus* (Galton, 1973a). In all other prosauropods the hind feet are proportionally much broader. The proximal part of metatarsal 1 is closely applied to metatarsal 2 (Figs. 11, 22E) and presumably it wraps around onto the dorsolateral surface. Metatarsals 2 and 3 are somewhat divergent as preserved (Fig. 12), but in life they were probably closer together (Fig. 22E). The articular surfaces of the metatarsals and phalanges are not exposed. Metatarsal 5 has a broad proximal part which has a longitudinally concave surface; the rest of the

ventral surface is gently convex. Metatarsal 5 may have lacked a phalanx,
but this was probably not the case because remains of a phalanx are pre-
served with the similarily shaped fifth metatarsals of *Anchisaurus capensis*
(Broom, 1906; Galton and Cluver, in press) and *"Hortalotarsus"* (Seeley,
1894). The first ungual phalanx is slightly smaller than that of the second
digit (Figs. 12, 22E). In all other prosauropods described to date the
first ungual is considerably larger than the second so that unguals 1 to 4
show a progressive decrease in size (Figs. 38A–E, F–I).

Ammosaurus major (Marsh)
Specimen 1, YPM 208 (Figs. 23–29)

IDENTIFICATION. This specimen is the holotype of *Anchisaurus major*
Marsh, 1889:331, the type species of the genus *Ammosaurus* Marsh,
1891:267.

PREVIOUS DESCRIPTIONS.
Anchisaurus major Marsh, 1889:331–332, fig. 1.
Ammosaurus major (Marsh) Marsh, 1891:267; 1892:545, pl. 16, fig. 4,
pl. 17, fig. 3; 1896:150, pl. 3, figs. 3, 6; Huene, 1906:15–19, pls. 5–9;
1907–08:303–304, figs. 297, 298; 1914a:13, 1914b:74–75, figs. 20–22,
1932:26–30; Lull, 1915:148–155, figs. 24, 25; 1953:123–129, figs. 19, 20;
Galton, 1971a:786–788, figs. 9, 11A.

LOCALITY AND HORIZON. As for YPM 1883, Manchester, Connecticut;
Portland Beds (p. 21).

MATERIAL. The main block is now in five pieces with the left hind limb (Figs.
23A, 27A, 28A, C), the right pes (Figs. 23B, 28B) and part of the sacrum
(Fig. 25A) fitting onto the large piece containing the last three dorsal ver-
tebrae and most of the pelvis (Figs. 23, 24). A block containing the missing
lateral part of the longitudinally sectioned right femur was discovered
during demolition of a bridge south of Manchester (p. 5). Although not
mentioned by Marsh, Lull or Huene, YPM 208 also includes a small block,
preparation of which exposed most of the right scapula (Fig. 25B), three
damaged dorsal vertebrae and parts of five dorsal ribs. No contacts can be
established between this block and the main block containing the pelvis and
hind limbs. The preserved part of the scapula (Fig. 25B) is similar to that
of *Anchisaurus* (Fig. 16C) except that the distal part is not twisted and the
proximal part appears to be proportionally broader. The dorsal ribs pre-

served on the surface of the block are stout with the width ranging from 8 to 10 mm. A sectioned centrum of a dorsal vertebra is 40 mm long and 20 mm high; so the dorsal centra are low as in YPM 209 (Fig. 2) and *Anchisaurus* (Fig. 15I).

SACRAL VERTEBRAE AND RIBS. The sacrum consists of three vertebrae (Figs. 24A, 25A, 26A, B), the last of which has plainly been incorporated from the caudal series. The articular surface of the prezygapophyses face dorsomedially. Those of the first sacral vertebra are slightly concave transversely but straight anteroposteriorly. The straight medial edge (Fig. 26A) forms a vertically inclined accessory articular surface, the zygantrum (cf. Fig. 4D). The other zygapophyses are poorly preserved. The neural spines are obliquely inclined backward and are incomplete dorsally (Fig. 26E). Apart from a slight depression at the distal end the dorsal surface of the first transverse process is flat (Figs. 24B, 26A). The anterior part of the second is also flat, but more posteriorly it is obliquely inclined, facing slightly posteriorly and covered with striations. The third transverse process curves slightly dorsally to meet the ilium and, unlike the others, it does not contact the sacral rib more distally (Figs. 26A, B, E). The dorsal and ventral surface are anteroposteriorly convex.

The centra were not firmly coossified because prior to preservation they shifted slightly relative to each other (cf. Figs. 25A, 26B). Proportionally the centra are low; for the first two centra the ratio of the combined length to the height is about 2.5 as against 1.8 for *Anchisaurus* (YPM 1883), 1.5 for *Efraasia* (SMNS 12667) and 1.0 for *Plateosaurus* (Huene, 1926). In ventral view (Figs. 25A, 26B) the successive centra are progressively broader. The second centrum has a median longitudinal depression; the third is transversely constricted and, judging from the position of the base of the postzygapophyses, less than 5 mm is missing posteriorly (Figs. 26A, B).

There are indications of the suture between each sacral rib and its centrum (Figs. 25A, 26B). The ventral surface of the first sacral rib (Figs. 25A, 26B) is gently convex anteroposteriorly but concave transversely with the expanded distal end slightly ventral to the under surface of the centrum. The anterior edge is sharp with a dorsoventrally concave anterior surface. The first sacral rib attached to the medial surface of the ilium near the base of the pubic peduncle. Transversely the ventral surface of the second sacral rib is slightly concave with a bifurcated proximal end which, along with the centrum, encloses a small foramen (Figs. 25A, 26B). Posteriorly the distal parts of the second and third ribs connect. The rodlike sacral rib and the transverse process of the third sacral vertebra share a massive base but then diverge. The rib is directed anterodorsally and slightly ventrally, the transverse process transversely and slightly dorsally (Figs. 24A, 25A, 26A, B, E). This lack of contact indicates that the third sacral
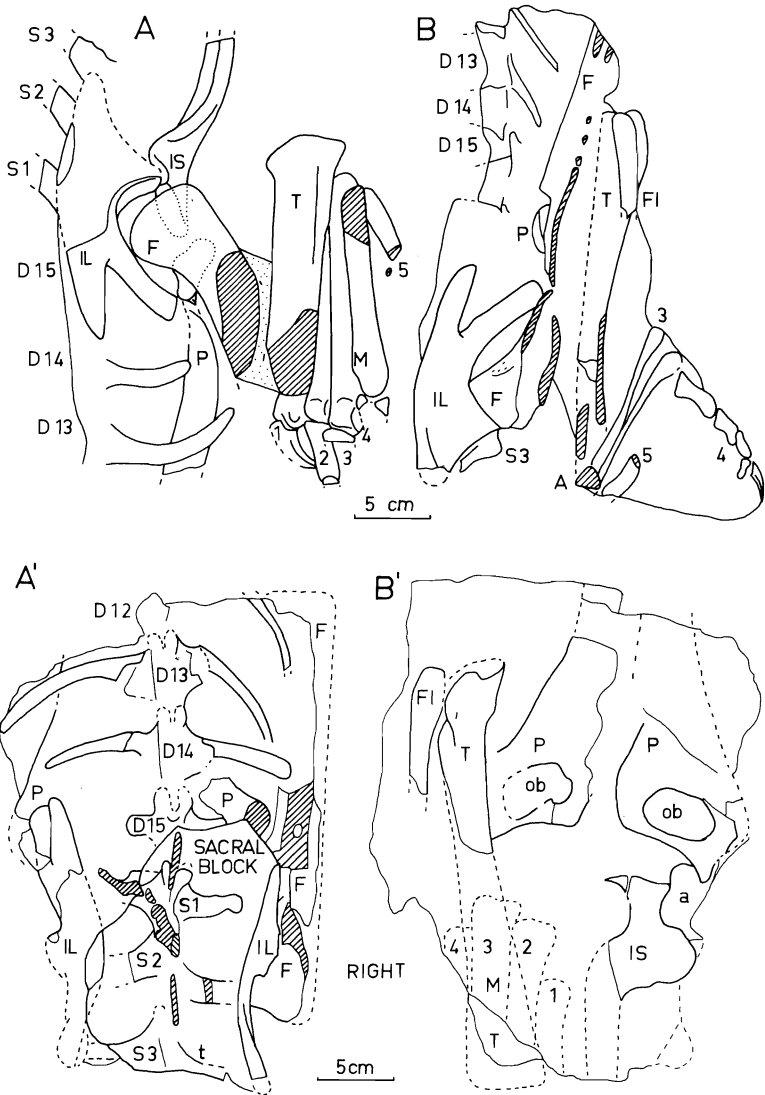
FIG. 23. *Ammosaurus major.* YPM 208 × 0.2. Pelvis and hind limbs as pre-served. *A*, left side; *B*, right side. Abbreviations for Figures 23 to 25: *A* = astragalus; *D* = dorsal vertebra; *F* = femur; *FI* = fibula; *IL* = ilium; *IS* = ischium; *M* = metatarsus; *P* = pubis; *R* = sacral rib; *S* = sacral vertebra; *T* = tibia; *a* = acetabulum; *ob* = obturator foramen; *t* = transverse process; *1-5* = digits; *4tr* = fourth trochanter. Broken bone indicated by cross-hatching.
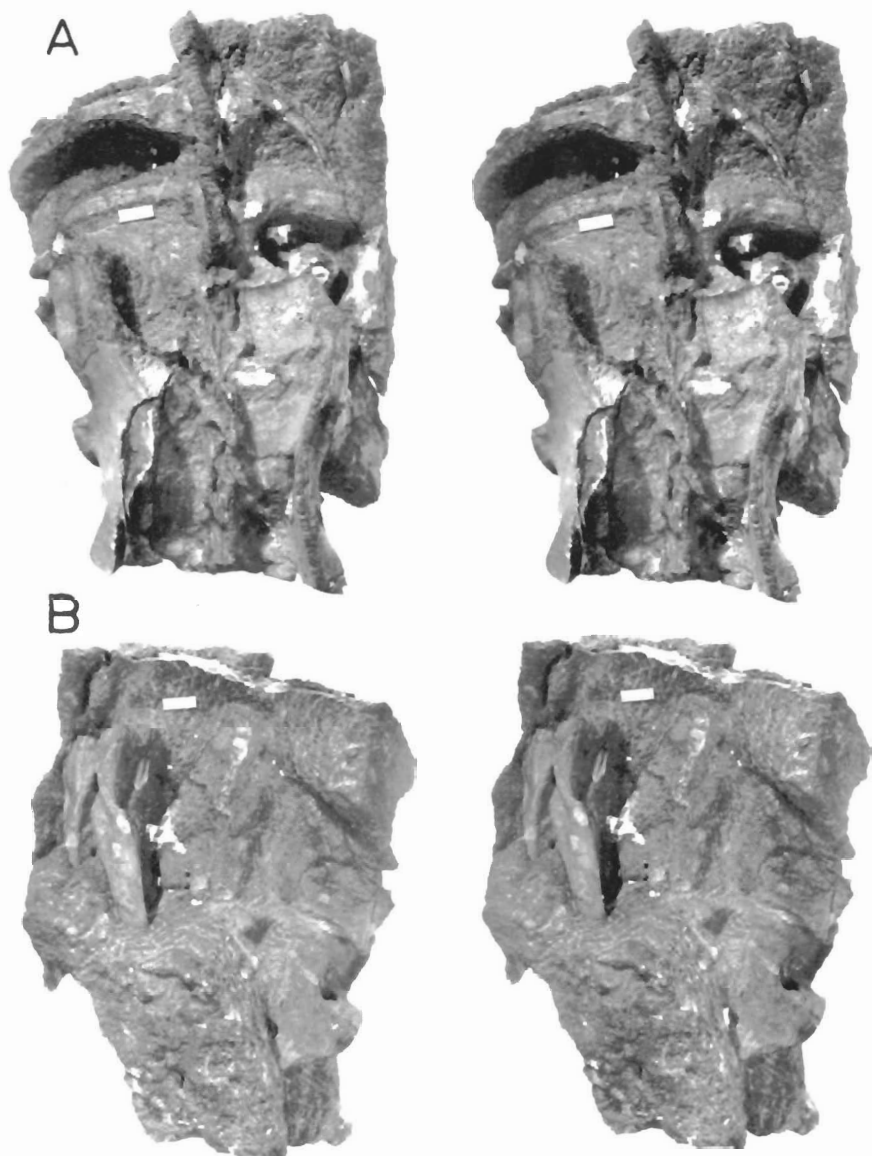
FIG. 24. *Ammosaurus major*. YPM 208. Stereophotographs of main block (*A*, *B*), with explanatory outlines (*A'*, *B'*) opposite page. *A*, dorsal view; *B*, ventral view. For abbreviations see Figure 23.
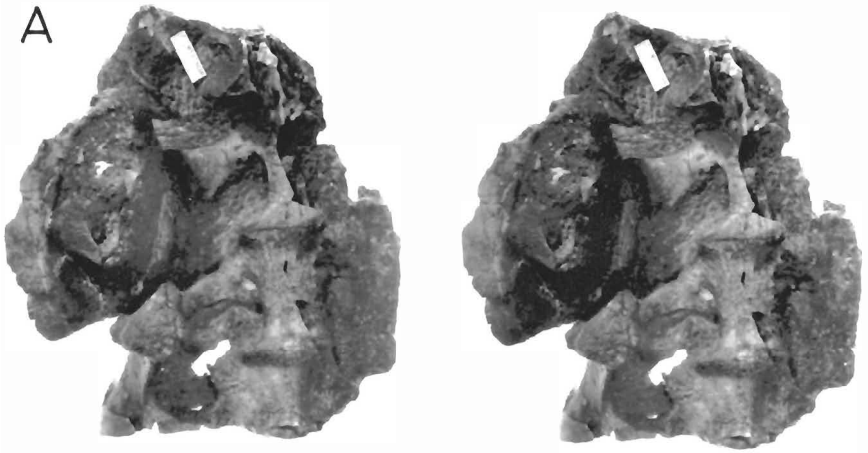
A

FIG. 25. *Ammosaurus major.* YPM 208. *A,* stereophotograph and explanatory outline, *A',* of the ventral surface of the "sacral block" (compare with Figure 24A'); *B,* left scapula in lateral view × 0.30; *C,* diagram of the main block in dorsal view to show bones visible at three different levels: ———, on dorsal surface (compare with Figure 24A); — — — , visible after removal of sacral block; .... on ventral surface (compare with Figure 24B);—·—·—·, determined by placing right pes (Fig. 28A) into metatarsal impressions on ventral surface of block (Fig. 24B); . . ., reconstruction.

vertebra was in the process of being incorporated into the sacrum. A similar lack of contact is shown by the anteriorly situated "new sacral rib" of some individuals (? male) of the ornithopod dinosaur *Hypsilophodon*: in one specimen deposition of bone between the new sacral rib and the transverse process resulted in a sacral rib of a normal form (Galton, 1974).

PELVIC GIRDLE. Apart from the elongate nature of the anterior process the ilium (Figs. 26A, B, E) of YPM 208 is of the normal prosauropod pattern. The dorsal edge of the ilium is sharp. Anteriorly the ventral edge of the anterior process is gently convex, but the process thickens posteriorly to form a ventrally facing and transversely straight surface that sweeps downwards to merge with the proximal part of the pubic peduncle. The peduncle is long (Fig. 26E) and broad (Figs. 26A, B) with a longitudinal dorsal ridge, the transverse curvature of which, more distally, continues onto the medial and lateral surfaces. More proximally the medial surface is flat and faces slightly dorsally whereas laterally a thin flange is developed (Figs. 26A, E) that increases the width of the acetabulum (Fig. 26B). The lateral surface at the base of the anterior process is concave and sweeps out to
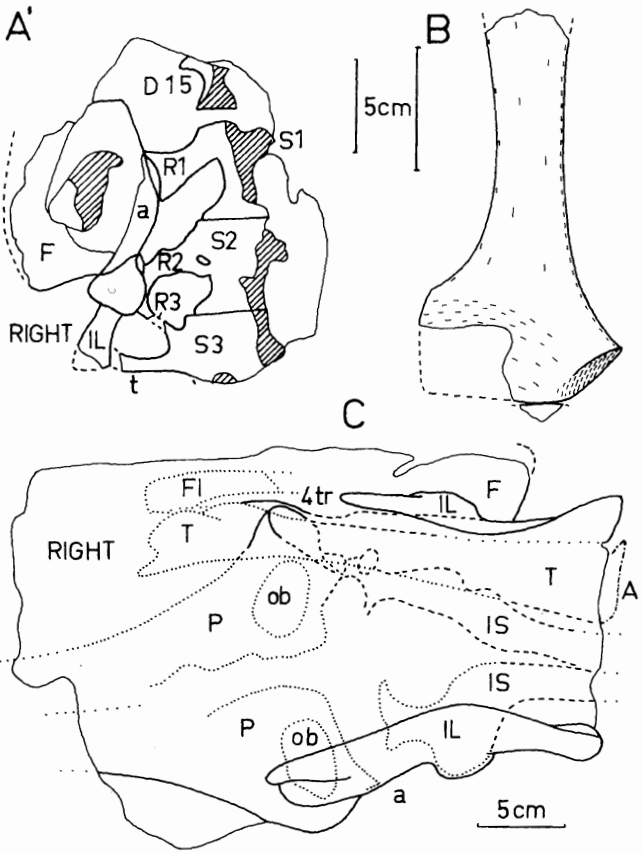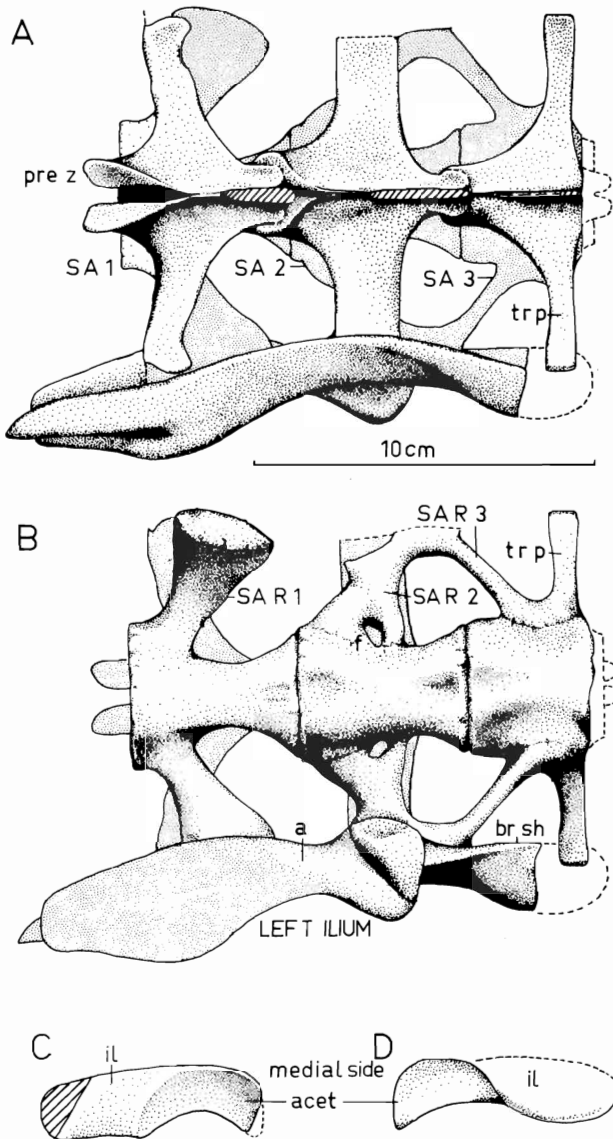
FIG. 26. *Ammosaurus major*. YPM 208. Reconstructions of sacrum and pelvic girdle × 0.45. *A*, sacrum and left ilium in dorsal view; *B*, sacrum and right ilium in ventral view; *C*, proximal end of pubis; *D*, proximal end of ischium; *E*, pelvic girdle and sacrum from left side; *F*, pubes and ischia in ventral view with shaded outline of ilia and sacrum; compare with *B*. Abbreviations: *SA* = sacral vertebra; *SA R* = sacral rib; *a* = acetabulum; *ap* = anterior process; *br sh* = brevis shelf; *F* = foramen; *il* = surface for ilium; *is* = surface for ischium; *obt for* = obturator foramen; *obt p* = obturator process; *p* = pubic peduncle; *pre z* = prezygapophysis; *tr p* = transverse process. Mechanically shaded areas in *A* and *B* restored from the opposite view.

E

SA 1
SA 3
a p
ILIUM
p
a
obt for
obt p
PUBIS
ISCHIUM

10 cm

obt
for
SA 1   SA 2

F   PUBIS
ISCHIUM
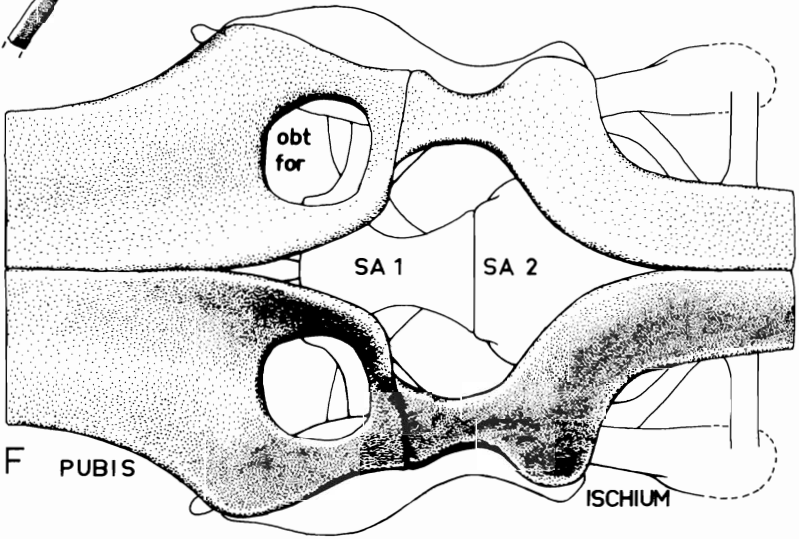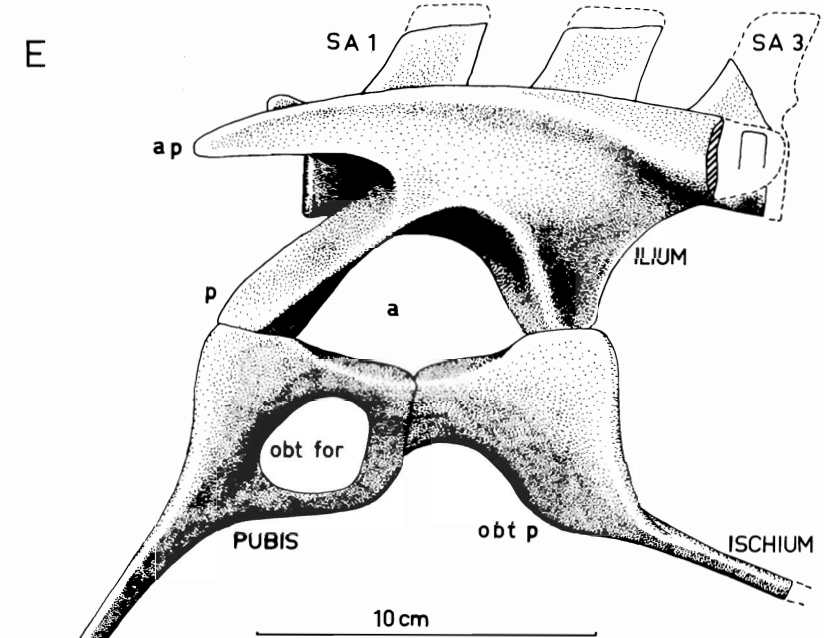
the edge of the acetabulum. The main blade of the ilium is also concave anteroposteriorly (Fig. 26A). Posteriorly there is a horizontal ridge along the side of the ilium. Ventral to this the surface is obliquely concave (Fig. 26E) with a sharp ventral edge. More dorsally there is an obliquely inclined surface that is delimited by a distinct edge and is covered with diagonally inclined striations (Figs. 26A, E). This surface was probably the main area of origin of the M. iliotibialis 2, while a M. iliotibialis 1 was probably differentiated on the long slender anterior process as was also the case in ornithischians (see Galton, 1969, 1970a). The acetabular surface (Fig. 26B) is wide and becomes progressively more concave laterally. The medioventral edge of the ilium is sharp, but most of the medial surface is hidden by matrix.

Both pubes have been compressed dorsoventrally but are plainly of the normal prosauropod pattern. The deep acetabular region with a large obturator foramen (plainly visible on the left, some of it on the right, Fig. 24B) is separated by a twisted region from the transversely oriented and broad-apron region, the distal part of which is missing. (Figs. 24B, 26E, F). The proximal subacetabular region has been reconstructed at 45° to match the angle of the corresponding part of the ischium. Proximally close to the ischium the pubis is very massive but the acetabular part is thinner, whereas the region posterior and ventral to the obturator foramen is very thin as is most of the apron region. The acetabular surface is concave anteroposteriorly (Fig. 26E) and transversely (Fig. 26C) with a sharp lateral edge.

The left ischium is practically undistorted (Figs. 23A, 24B) and further preparation showed that the subacetabular region is remarkably shallow for a prosauropod (Figs. 26E, F). The minimum depth is 21 mm with a 45 mm long contact with the pubis, the corresponding edge of which is 62 mm with a subacetabular depth of 78 mm. The anterior part of the ventral edge is well formed and undamaged; so this edge did not border a foramen. More posteriorly the edge is broken (Fig. 24B), but there appear to be indications of an obturator process, the outline of which was probably as shown (Figs. 26E, F). The proximal part of the ischium adjacent to the ilium is thick and tapers ventrally. The acetabular surface is concave anteroposteriorly and transversely and is delimited laterally by a sharp edge. The thick posterior edge has a prominent groove which more distally spreads out onto the dorsal surface. The M. ischiotrochantericus probably originated from the groove and the dorsal surface of the ischial rod. The broken end of the ischial rod is suboval in cross section with a sharp lateral edge.

HIND LIMB. Both femora are incomplete (Figs. 23, 25C, 27A) and breaks show that the walls were thin as are those of the fibula, tibia, and meta-
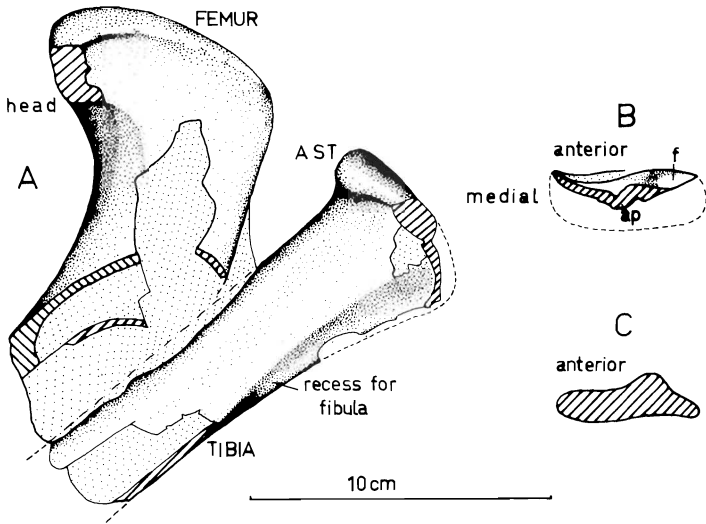
FIG. 27. *Ammosaurus major.* YPM 208. Right femur and tibia × 0.4. *A*, in lateral view; *B*, dorsal view of right astragalus; *C*, vertical section through right astragalus. Abbreviations: *ap* = ascending process; *ast* = astragalus; *f* = depression for fibula. Broken bone shown by cross-hatching and matrix by stipple.

tarsals. The large head of the left femur is transversely expanded (Figs. 25C, 27A) with a broad dorsal surface for the articular cartilage and a rough medial area for the ligaments that held the head in the acetabulum (Fig. 27A). The fourth trochanter is large and it is on the proximal half of the femur (Figs. 24A, 25C). The right femur is crushed dorsoventrally (Fig. 23B) and the lateral part, recently discovered in the now demolished bridge in south Manchester, does not add anything to the picture. Parts of the two distal condyles and some of the intercondylar area are preserved; so originally the femur was slightly longer than the present length of 280 mm.

The right tibia is slightly displaced, the proximal end is crushed, and the distal end is missing (Figs. 23B, 25C). The cnemial crest is large with a sharp edge that continues distally as the medial edge of the bone. The position of the distal end can be located by the astragalus that is with the pes, the metatarsals of which fit onto their natural mold on the lower surface of the main block (Figs. 23B, 24B). The combined length of the tibia and astragalus is 280 mm. Consequently the length of the tibia at slightly less than 280 mm was shorter than the femur. The distal part of the left tibia is transversely expanded with a well-developed depression for the

fibula on the lateral surface (Fig. 27A). The edge backing this depression becomes less acute more proximally and merges with the shaft at about midlength. In *Anchisaurus* (Fig. 22B), *Efraasia* (Galton, 1973a) and *Plateosaurus* (AMNH 6810) this depression is much less pronounced. The fibula is represented only by the anteroposteriorly expanded proximal end and part of the shaft (Fig. 24B).

The left astragalus has been obliquely sectioned through the middle of the large ascending process (Figs. 27B, C, 28A) that probably keyed into the tibia as in *Anchisaurus* (Fig. 22B). There are indications that this was the case for the much flattened right astragalus (Fig. 27A), the distal articular surface of which is anteroposteriorly convex. The figure of the pes given by Marsh (1889, 1896) includes the fibula, calcaneum, and three distal tarsals. The fibula is reconstructed, but Lull (1915, 1953) mentions the other elements. However, there is no trace of the calcaneum (Figs. 27A, 28A, B) and only two badly damaged distal tarsals can be identified (Figs. 28A, B, 29D). It should be noted that Marsh's figure of the pes of *Ammosaurus* is incorrectly given by Romer (1956, fig. 191C; 1966, fig. 228A) as that of *Yaleosaurus*.

The metatarsus is very broad (Figs. 28, 19D) in comparison with that of *Anchisaurus* (Fig. 22E) and both feet are slightly distorted. The first metatarsal is broad and stout with a transversely expanded distal end (Fig. 28B, 29D). The articular surfaces of metatarsals 1 to 4 are well defined as are the adjacent striated crescentic areas that were the area of origin for the extensor tendons (Figs. 28A, B, 29D). Metatarsal 5 is small, slender and tapers to an oval cross section and the articular surface is not preserved.

The first phalanx of the first digit is slightly twisted so that the first ungual faces slightly medially (Figs. 28B, 29D). Lull (1915, 1953) criticized the figure of the foot given by Marsh (1889, 1896) because the hallux was probably rotated to the rear rather than being anteriorly directed as shown by Marsh. However, this reorientation of digit 1 was based on a correlation with the footprints of *Anchisauripus exsertus* which is impossible (Galton, 1970a, 1971a). The first ungual has a large ventral area for the attachment of the flexor tendons (Figs. 29A, B) and it is the largest with unguals 1 to 4 showing a progressive decrease in size (Fig. 29D). The phalanges are broad and stout and, although crushed and broken to a varying extent (Fig. 28), the reconstructions are reasonably accurate (Fig. 29D). The rudimentary phalanx of digit 5 is represented by a fragment of bone close to the left fifth metatarsal (Fig. 28B) and the reconstructed outline is based on MNA G2 7233 (Figs. 35B, 38A).

Ammosaurus major
Specimen 2, YPM 209 (Figs. 2A, 30–31)

IDENTIFICATION. This specimen, the holotype of *Anchisaurus solus* Marsh, 1892:545, is here referred to *Ammosaurus major* (Marsh).

PREVIOUS DESCRIPTIONS.
Anchisaurus solus Marsh, 1892:545; 1896:149–150; Huene, 1914b:72–74, figs. 12–19; Lull, 1915:144–148, figs. 22, 23; 1953:120–123.
Anchisaurus (?) solus Marsh, Huene, 1906:14–15, pl. 4.
Ammosaurus solus (Marsh) Huene, 1932:27–30, pl. 49, fig. 1.
Ammosaurus major (Marsh) Galton, 1971a:786–788. fig. 11A.

LOCALITY AND HORIZON. As for YPM 1883 and 208, Manchester, Connecticut: Portland Beds (p. 21).

MATERIAL. An almost complete skeleton (Figs. 30–31) of a young individual with an estimated length of about 1 m as against 3 m for YPM 208. Only the distal part of the tail and the right lower arm are missing but unfortunately the bones are rather poorly preserved.

SKULL. The position of the premaxilla is indicated by three teeth that are inclined slightly posteriorly (Fig. 31B). The crown of the third tooth is only slightly expanded anteroposteriorly and the tip is quite acute. There is room for two more teeth (to give a premaxillary count of five as in *Anchisaurus* and *Plateosaurus*) between this tooth and the fragmentary remains of the roots of the five most anterior maxillary teeth. The form of the maxilla is rather indeterminate, but the concave posterior edge may represent part of the margin of the antorbital fenestra (cf. Figs. 13A, 31B).

The skull is preserved with the jaws closed, the anterior upper and lower teeth preserved in close proximity (Fig. 31B). The two mandibular rami meet at an angle of about 30° and this is probably natural. The right mandibular ramus is preserved as a longitudinal vertical section and the preserved length of 65 mm represents the complete length. The jaw is slender with a low coronoid process. Anteriorly there are indications of five teeth (Fig. 31A) that are directed slightly anteriorly as in *Anchisaurus* (Fig. 13A).

The rest of the skull was disarticulated during or prior to burial and very little is preserved (Figs. 30B, 31B). Marsh (1892, 1896) and Huene (1932) thought that the orbits were large, but there is no definite evidence that this was the case. Two sectioned bones (F, Figs. 30A, 31B) may be
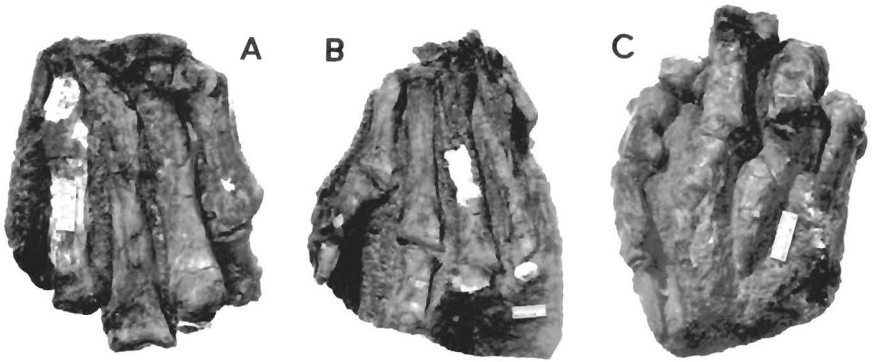
FIG. 28. *Ammosaurus major*. YPM 208. Stereophotograph of pes in dorsal view. *A* = right metatarsus; *B* = left pes; *C* = phalanges of right pes.

the frontals as Huene (1914b) indicated, but they could equally well be the parietals; the identification of the right jugal is equally tenuous.

VERTEBRAL COLUMN. The junction between the cervical and dorsal series is, as Huene (1906) pointed out, indicated by a change in the lengths of the centra (Fig. 30B). The length of the centrum of the last cervical vertebra is 18 mm, while that of the first dorsal is 14 mm. Eight vertebrae are clearly visible anterior to this junction and there are indications of the axis and atlas on the skull block (Figs. 30B, 31B). This gives a cervical count of 10 as in *Plateosaurus* (Huene, 1926) and *Efraasia* (Galton, 1973a). Huene (1906, 1914b, 1932) thought that there were 9 cervicals and 14 dorsals, 13 of which were visible with one hidden by the matrix supporting the apron region of the pubis. However, the pelvic girdle is in natural articulation as are the dorsal and caudal series on either side of it. Assuming that the sacrum occupied the same relative position as it does in YPM 208, then there is sufficient room for two more dorsal vertebrae, the second of which is shorter as in *Plateosaurus* and *Efraasia*, between dorsal 13 and the presumed position of sacral 1.

The first five vertebrae are disarticulated to a varying degree (Figs. 30A, 31A), but the rest of the vertebral column is in natural articulation (Fig. 30A). The separation between the individual centra is quite marked, being about 6 mm for the posterior cervicals, and the anterior dorsal and about 3 mm for most of the other dorsals and the caudals. The ends of the centra are not well formed, consisting of very porous bone; so in life the ends were probably continued in cartilage. The wider spacing of the cervicals is probably a result of the very marked amphicoely of the centra in prosauropods (see below for Navajo material of *Ammosaurus*). Sections of the caudal vertebrae show that the centra are hollow with thin walls.
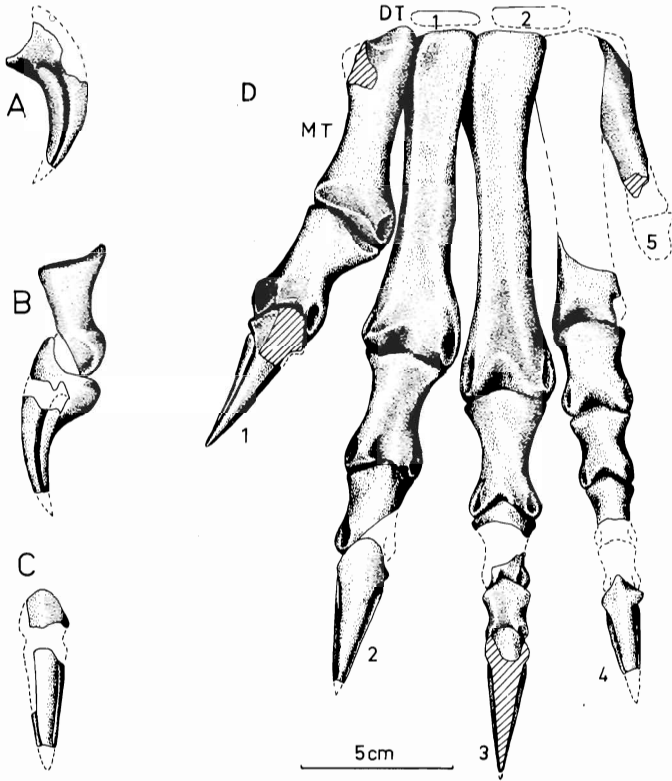
FIG. 29. *Ammosaurus major*. YPM 208. Pes × 0.4. *A*, left ungual phalanx digit 1 in medial view; *B*, phalanges of digit 1 of right pes in medial view; *C*, right ungual phalanx digit 1 in dorsal view; *D*, reconstructed left pes in dorsal view. Abbreviations: *DT* = distal tarsals; *MT* = metatarsus.
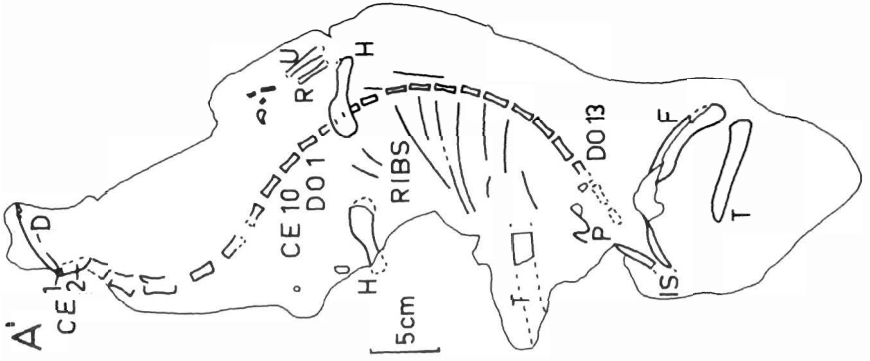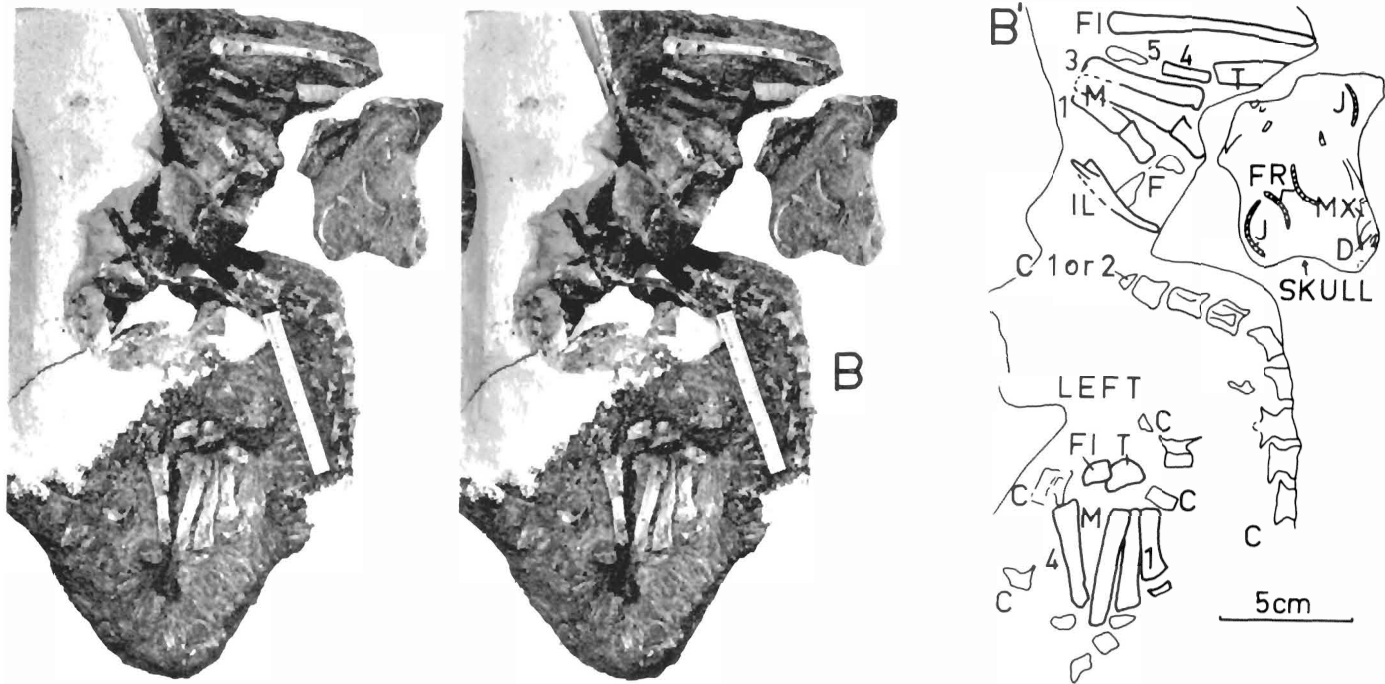
FIG. 30. *Ammosaurus major*, juvenile. YPM 209. Stereophotographs (*A*, *B*) and explanatory outlines (*A'*, *B'*). *A*, ventral view of block; *B*, dorsal view of anterior and posterior parts of block. For abbreviations see Figure 31.
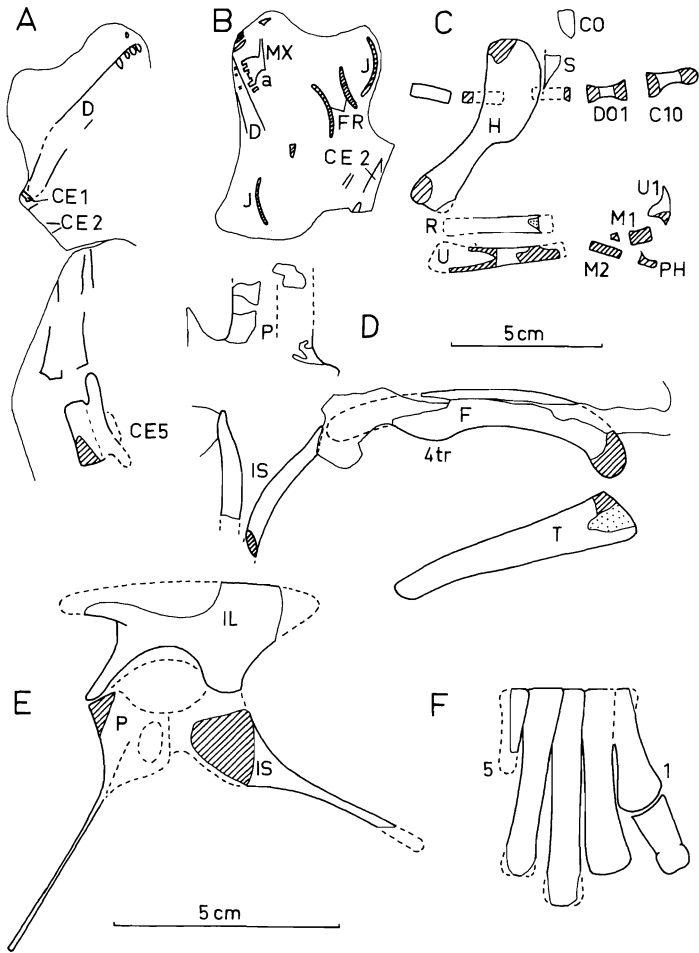
FIG. 31. *Ammosaurus major*, juvenile. YPM 209. A, right mandible with anterior cervical vertebrae; B, skull block; C, left forelimb; D, pelvis and left hind limb; E, pelvic girdle from left side; F, left pes in ventral view. A–D as preserved × 0.4; compare with Figure 30A; E, F, reconstructions × 0.6. Abbreviations for Figures 30 and 31: C = caudal vertebra; CE = cervical vertebra; CO = coracoid; D = dentary; DO = dorsal vertebra; F = femur; FI = fibula; FR = frontal; H = humerus; IL = ilium; IS = ischium; J = jugal; M = metatarsus; M1 = metacarpal 1 or phalange 1 of digit 1; M2 = metacarpal 2; MX = maxilla; P = pubis; PH = phalange; R = radius; S = scapula; T = tibia; U = ulna; U1 = ungual 1; 1–5 = digits 1 to 5; 4tr = fourth trochanter; a = antorbital fenestra. Broken bone indicated by cross-hatching.

PECTORAL GIRDLE AND FORELIMBS. Adjacent to the proximal end of the left humerus there are two pieces of bone that are parts of the left coracoid and scapula (Figs. 30A, 31C). The lateral surface is exposed and the rest of the scapula is presumably underneath the humerus.

The left humerus (Figs. 30A, 31C) is nearly complete and is undistorted. The lateral surface of the proximal end is gently convex longitudinally and concave transversely; the latter curve is more marked distally so that the deltopectoral crest is anteriorly directed. The deltopectoral crest is large with its tip on the proximal half of the humerus. The shaft is gently convex anteroposteriorly and is twisted so that the articular condyles are set at an angle of about 45° to the proximal end. The outer or radial condyle appears to be larger than the inner condyle. Eroded parts show that the humerus is hollow and thin walled; this is also true for the radius, ulna, femur, tibia, fibula, and metatarsals.

The manus is poorly preserved, but the large ungual phalanx of the first digit is almost complete and is 15 mm long (Figs. 30A, 31C). Close to it is part of the first phalanx, but there is no trace of the metacarpal. Part of the second (possibly third) metacarpal shows that it was slender and elongate. The longitudinal and dorsoventrally oriented section through two phalanges (digit 2 or 3) shows that they are small (lengths 4 mm, 5 mm).

PELVIC GIRDLE. The acetabulum was oval (Fig. 31E) as in other prosauropods because the ilium has a long pubic peduncle, the lateral edge of which flares out to form a broad acetabular surface. The central part of the main blade region is preserved as an impression and, judging from the curves, this region was markedly concave longitudinally as in YPM 208 (Figs. 26A, E) and *Anchisaurus* (Fig. 19A). The posterior edge is eroded and only a small part of the dorsal edge is preserved so that exact outline of the ilium and the length of the anterior process cannot be determined. However, it was probably quite long and, judging from the preserved part of the dorsal edge, it was probably slender as in YPM 208 (Fig. 26E) and *Anchisaurus* (Fig. 19A). The dorsal edge of the anterior tip is definitely eroded and it is not the natural edge as indicated by Huene (1914b, fig. 16) and Lull (1915, fig. 23).

Some of the apron region of the pubis is preserved (Figs. 30A, 31D) and it is broad and transversely oriented. The ventral surface of the apron region of the right pubis is straight along the length (Fig. 31E) and gently convex transversely. As preserved the apron region is pushed towards the vertebrae and there is a crack across the basal region. In the reconstruction the apron is shown directed more ventrally (Fig. 31E).

Both ischia are rather incomplete (Figs. 30A, 31–D, E) and are twisted along their length. The proximal part is at an angle of about 30° to the

vertical. The ischial rods are horizontal, oval in cross section with sharp edges (Figs. 30A, 31D). The combined width of the ischial rods is 14 mm compared to about 26 mm for the apron region of the pubis.

HIND LIMB. The left femur and tibia are visible in medial view (Figs. 30A, 31D). A split passes along the length of the femur, the proximal end of which is missing. The fourth trochanter is large with a rugose area on the proximal part of the trochanter and the adjacent part of the shaft as in YPM 208 and AM 41/109 (see p. 17). The shaft is gently bowed and circular in cross section. The preserved length is 84 mm and, as there is no trace of bone in the rock around the proximal end (Figs. 30A, 31D), the maximum length possible was 110 mm. If the femur was this length then the fourth trochanter would still have been in a slightly more proximal position than is usually the case in prosauropods. However, this is not unexpected because this was obviously a very young individual as shown by the small size (estimated length 1 m) and the incompletely ossified ends of the bones. The fourth trochanter of young individuals of the ornithopods *Dysalotosaurus* (Janensch, 1955) and *Hypsilophodon* (Galton, 1974) is more proximally placed than it is in older individuals.

The left tibia (Figs. 30A, 31D) is complete and has a length of 92 mm so it was almost certainly shorter than the femur rather than longer as Huene (1932) thought. The cnemial crest is continued more distally as a sharp edge that passes diagonally across the shaft to merge with the medial edge. The distal end (Fig. 30B) is transversely expanded with a depression to receive an ascending process from the astragalus. Both fibulae are preserved, but only the right is exposed (Fig. 30B). The bone is slender and the proximal end is missing.

The astragalus may be represented by a piece of bone near the left foot (Fig. 30B) but there is no sign of the calcaneum or the distal tarsals. Both metatarsi are damaged (Fig. 30B) but it is apparent that the foot is of the broad pattern (Fig. 31F), resembling that of *Ammosaurus* (Fig. 29D) more closely than that of *Anchisaurus* (Fig. 22E). The resemblance is especially true of the first metatarsal, the distal end of which is transversely expanded (Figs. 30B, 31F).

<div align="center">

Prosauropod, generically indeterminate
YPM 2125 (Fig. 32)

</div>

PREVIOUS DESCRIPTIONS. Unidentified by Smith, 1820; Hall, 1821; Hitchcock, 1841:503, pl. 49, figs. 66–68; Wyman, 1855; identified as *Anchisaurus colurus* by Lull, 1912:411; 1915:77 and Huene, 1914a:3; identified as *Yaleosaurus colurus* by Lull, 1953:60.
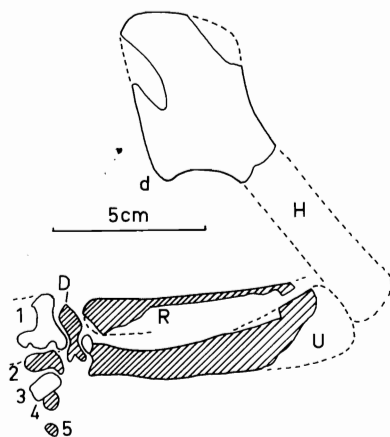
FIG. 32. Prosauropod right forelimb × 0.4. YPM 2125. Abbreviations; D = distal carpal; H = humerus; R = radius; U = ulna; d = deltopectoral crest; 1-5 = metacarpals 1 to 5. Broken bone indicated by cross-hatching.

LOCALITY AND HORIZON. East Windsor, Connecticut, found 18 feet below top of rock while blasting for a well, from the Portland Beds of Newark Series.

MATERIAL. This specimen was discovered in 1818. Smith's (1820) description made it the first fossil bone recorded from the Triassic of the Connecticut Valley and, although not realized at the time, one of the earliest records of a dinosaur from anywhere in the world. The specimen includes eight pieces of matrix with fragmentary remains of caudal vertebrae including a sectioned series of three vertebrae from the middle part of the tail. Another block contains the distal end of the left femur with traces of the fibula and a natural mold of part of the tibia. The distal width of the left femur is about 40 mm and there is practically no intercondylar groove. The main block has the articulated but rather incomplete forelimb exposed in medial view (Fig. 32). The proximal part of the humerus is flattened and there is no trace of the distal half. The radius and ulna are longitudinally sectioned and are rather incomplete. The manus shows the remains of two distal carpals, one of which is very large, plus an enormous first metacarpal and traces of the other four. The bones are intermediate in size to those of AM 41/109 and YPM 1883. The structure of the forelimb is prosauropod, but metacarpals 2 to 5 are so fragmentary that it is impossible to determine whether the manus was of the slender type (referable to *Anchisaurus*) or

the broad type (referable to *Ammosaurus*). I conclude that this specimen is from a generically and specifically indeterminate prosauropod dinosaur.

Prosauropod material from Arizona
Ammosaurus cf. *major*
MNA G2 7233

PREVIOUS DESCRIPTIONS. Brady, 1935, 1936; Galton, 1971a: 782–783, figs. 1–3.

LOCALITY. Found by Brady (1935, 1936) on the Navajo Indian Reservation, northeastern Arizona, about two and a half miles east of Inscription House Lodge (on road between Tuba City and Navajo Mountain) on the plateau between Navajo and Shonto Canyons.

HORIZON. Near top of the Glen Canyon Series in typically cross-bedded Navajo Sandstone about 80 to 100 feet below the top of the formation.

MATERIAL. Brady (1935) noted that the specimen was preserved as it died in a prone position with the hind limbs doubled under it, the feet extended and the claws gripping the sand. However, erosion removed much of the skeleton before its discovery (Fig. 33A) and the specimen now includes gastralia, several incomplete caudal vertebrae, two unguals of the manus, the apronlike part of the pubes, the right tibia, and both hind feet (Figs. 33B, 34F–J, 35B, 36L, M, 37, 38A–E, Table 4).

UCMP 82961

PREVIOUS DESCRIPTION. Galton 1971a:783–784, figs. 4–6.

LOCALITY. Found by M. Wetherill on the Navajo Indian Reservation 300 yards east of the road to the Betatakin Ruin 7.7 miles from the Kayenta-Tuba City road.
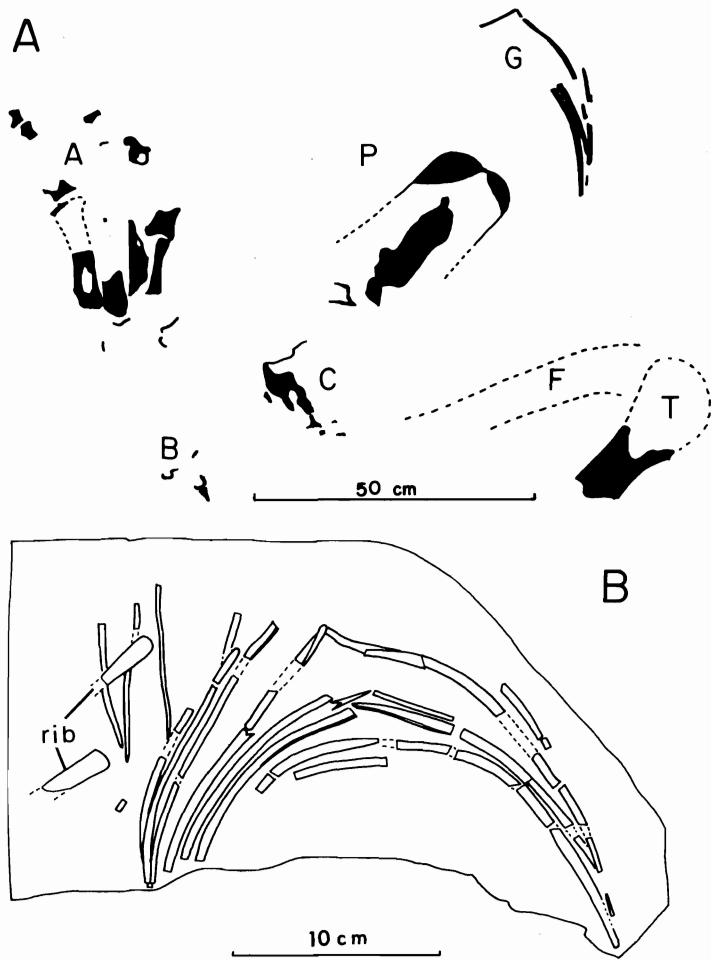
HORIZON. Navajo Sandstone.

FIG. 33. *Ammosaurus.* MNA G2 7233. *A*, specimen as found, after Brady (1935); *B*, gastralia. Abbreviations: *A* = left pes; *B*, *C* = caudal vertebrae; *F* = femur; *G* = gastralia; *P* = pubes; *T* = tibia.

MATERIAL. The specimen consists of two cervical vertebrae, the right manus, the ungual phalanges from both hind feet (Figs. 34A–E, 35A, 36A–K, 38F–L, Table 4) plus a drawer of talus slope debris, most of which proved to be an insolvable jigsaw puzzle.

DESCRIPTION. See figure captions for specimen numbers.

VERTEBRAE. From a comparison with the neck of *Plateosaurus* (AMNH 6810 and Huene, 1926) it would appear that the sixth and the eighth cervical vertebrae (Figs. 34A–E) are represented. The sixth cervical vertebra (Figs. 34D, E) has been restored to a certain extent because the anterior end was broken off and separated a little before preservation and the ends of the centrum are slightly distorted and broken. The eighth cervical vertebra (Figs. 34A–C) is less complete and the right side has been restored as a mirror image of the left. The centrum is very compressed laterally (Fig. 34C) and markedly amphicoelous with the concavity at each end being at least 10 mm deep. The concavity is also large so that the bone at each end of the centrum is thin. The laterally facing parapophysis is on a tapering ridge that more posteriorly becomes sharp edged and then merges with the centrum (Figs. 34A, B). The surface above and below this ridge is dorsoventrally concave. There are indications of the neurocentral suture on both vertebrae. The diapophysis is anteroventrally and laterally directed and it is borne on a long process that is dorsoventrally flattened. There is a well-defined groove along the lateral edge of the postzygapophysis (Fig. 34B) as in *Plateosaurus* (AMNH 6810).

The ribs of both cervical vertebrae were held parallel to the long axis (Figs. 34A, D) and those of the eighth (Fig. 34E) were more ventrally directed than those of the sixth cervical vertebra (Fig. 34B). The original length of these ribs is not known but alongside two-thirds of the left rib of the sixth cervical vertebra there is the slender distal part of another rib. The complete rib was probably about 75% longer than shown (Fig. 34A) so that it was about twice the length of the centrum as in *Plateosaurus* (AMNH 6810). It should be noted that the cervical ribs are shown too ventrally directed in the reconstruction of *Plateosaurus* by Huene (1926, pl. 7; in Romer, 1966, fig. 230) and they should be more parallel to the vertebrae as in AMNH 6810 (Fig. 2B; Colbert, 1961, pl. 29).

There are several incomplete caudal vertebrae and the reconstruction (Fig. 34F–H) is based on three adjacent anterior caudal vertebrae. There are traces of the suture between the neural arch and the centrum. Proportionally the centrum is not as high as in *Plateosaurus* (Huene, 1926) and in this respect resembles that of *Ammosaurus* (YPM 209, Fig. 30B). A more posterior but rather incomplete caudal vertebra is also shown (Fig. 34I). An almost complete chevron (Fig. 34J) from an anterior caudal
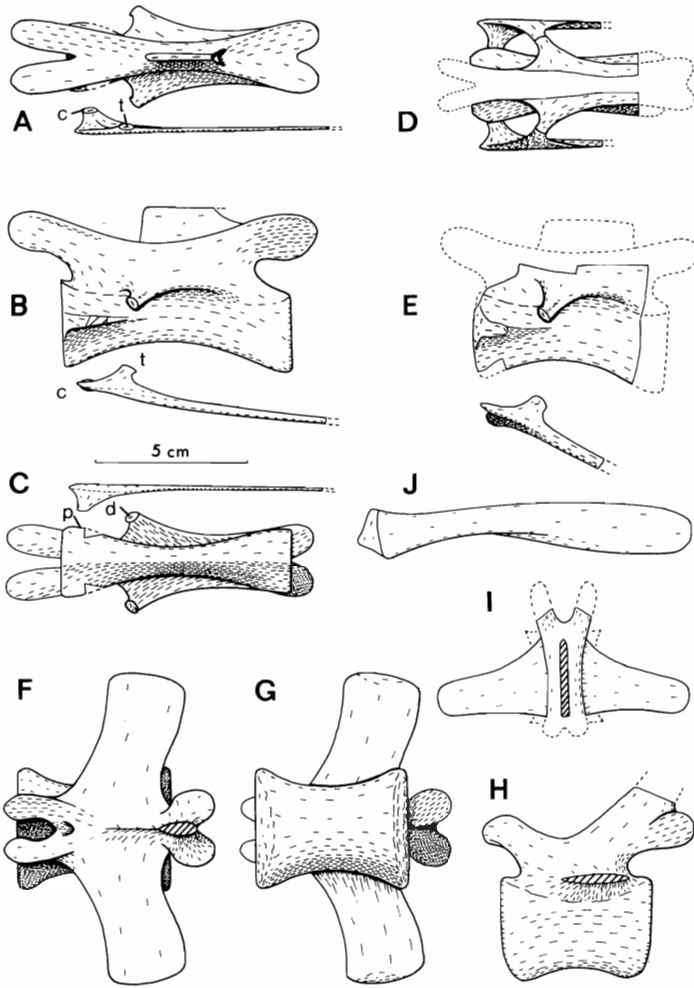
FIG. 34. *Ammosaurus.* Vertebrae × 0.4. Sixth cervical vertebra with rib: *A*, dorsal view; *B*, lateral view; *C*, ventral view. Eighth vertebra with rib: *D*, dorsal view; *E*, lateral view. Anterior caudal vertebra: *F*, dorsal view; *G*, ventral view; *H*, lateral view. *I*, Caudal vertebra from anterior third of tail in dorsal view; *J*, chevron from anterior caudal vertebra. *A–E*, UCMP 82961, *F–J*, MNA G2 7233. Abbreviations: *c* = capitulum; *d* = diaphysis; *p* = paraphysis; *t* = tuberculum.

vertebra has a bladelike lower half that is laterally compressed.

The distal ends of two dorsal ribs are preserved on a block with several gastralia (Fig. 33B) that, judging from their position as found (Fig. 33A), are from the posterior part of the abdominal cuirass. The individual rods are up to 100 mm in length, about 5 mm wide, 2 mm thick, and oval in cross section; some have a groove along the posterior edge. The gastralia resemble those of the more complete cuirasses of *Efraasia* (Galton, 1973a, pl. 2) and *Plateosaurus* (Huene, 1932, fig. 8, pl. 32).

MANUS. This is well preserved (Figs. 35A, 36A) in ventral view. The first distal carpal (Figs. 35A, 36A–C, E) is 31 mm wide and 21 mm high with a maximum thickness of 0.8 mm. The dorsal edge is thin and the ventral edge is thick, forming a gently convex surface with a lateral depression (Figs. 35A, 36A–C). The smaller element is probably the second distal carpal; it is about 14 mm wide and the ventral surface forms a twisted plane. The first metacarpal is slightly crushed (Figs. 35A, 36A–E), but its general appearance is not distorted. The proximal surface is gently concave ventromedially (Fig. 36E). The lateral surface of the proximal part is concave to receive the second metacarpal (Figs. 35A, 36A). The ginglymus is asymmetrical (Figs. 36B–D), being diagonally inclined, so that the first phalanx was held ventromedially with the metacarpals held horizontally. The first phalanx is also asymmetrical (Figs. 36F–K) so that during flexion the ungual phalanx moved ventrolaterally. The enormous ungual phalanx has a large ventral area for flexor tendons and a prominent dorsal process for extensor tendons (Fig. 38J). There is a slight asymmetry so that the medial edge is slightly more dorsal than the lateral edge (Fig. 38J). The ventral surface is gently convex (Figs. 35A, 36A). The appearance and proportions of the other metacarpals and phalanges are shown (Figs. 35A, 36A). The ungual phalanges of the second and third digits are much smaller and less trenchant than that of the first digit. The manus of MNA G2 7233 is represented by two damaged ungual phalanges (Figs. 36L, M) that, on account of their small size, are probably from the second and third digits (cf. Fig. 36A).

PELVIC GIRDLE. Only the basinlike anterior part of the pubes is preserved as an impression of the ventral surface with a partial layer of thin bone (Figs. 33A, 37A). The pubes are broad with a combined width of 108 mm distally and widen to at least 120 mm more proximally. At the distal end of each pubis there is a well-marked swelling of the ventral surface similar to that on the pubis of *Anchisaurus* and *Efraasia* (Figs. 20A, E). At the proximal end of the left pubis there are indications of a small obturator foramen (Fig. 37A) and the adjacent bony surface is obliquely inclined,
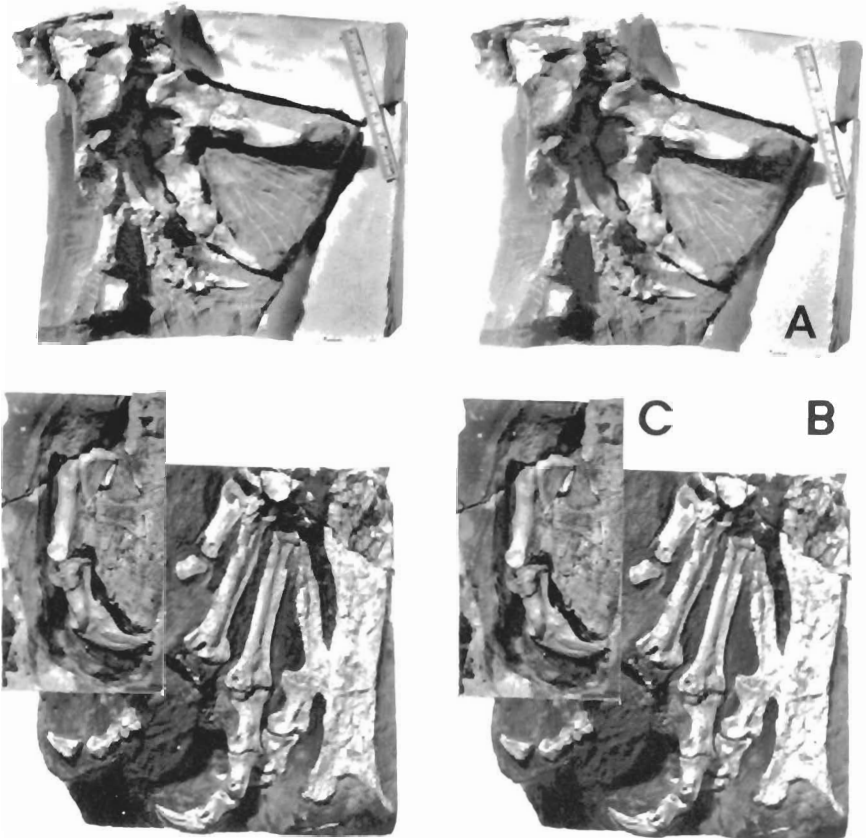
FIG. 35. *Ammosaurus*. *A*, stereophotograph of left manus of UCMP 82961 in ventral view; compare with Figure 36A; *B*, stereophotograph of right pes of MNA G2 7233 in dorsal view; compare with Figure 38A; *C*, as *B*, digit 1 in ventral view. Scales represent 7 cm.

facing posteromedially and dorsally as does the equivalent area in *Efraasia* (Fig. 20D).

HIND LIMB. Brady (1935:213) wrote that "the femur has a marked sigmoidal curve and is about 30 cm. in length; the tibia and fibula are each 20 cm. in length and 3.5 and 2.5 cm. in width respectively at the middle of the shaft and have very thin walls." The femur was not listed by Brady (1935, 1936) among the elements collected and it is not at the Museum of Northern Arizona. The tibia is rather badly crushed (Fig. 35B) and most of the fibula is no longer preserved (cf. Figs. 35B, 37B). Apparently there was a typographical error because, on the basis of a photograph of the bone *in situ* (Fig. 37B), the tibia was about 28 cm long and it actually measures 28.3 cm. The small calcaneum appears to have been complete (Fig. 37B) but most of the astragalus was missing. Brady (1935) illustrated the left pes (Fig. 37C) but the more complete and undescribed right pes (Fig. 35B) was collected later (Brady, 1936). The bones of both feet are rather crushed and some of the phalanges are missing, but the general proportions, including those shown by dashed lines, are reasonably correct (Fig. 38A). The medial half of the first distal tarsal is preserved (Fig. 38A); the ventral edge is sharp and the proximal surface is gently concave as is that of the second distal tarsal of the right foot. The lateral part of the first phalanx of the first digit is crushed, as is the proximolateral part of the ungual phalanx so the exact articulation of the ungual phalanx cannot be determined. The ungual phalanges of digits 1 to 4 show a progressive decrease in size (Figs. 38A–E). The ungual phalanx of the first digit has a large ventral area for the flexor tendons (Fig. 38B) and this phalanx is asymmetrical, curving slightly medially (not well shown in Figure 38A) and the ventral surface is obliquely inclined so that it faces ventrolaterally (Fig. 35B). The gently rounded lateral edge is more dorsal than the more acute medial edge (Fig. 38B) and the lateral claw groove is more dorsal than the medial one. The ungual phalanges of digits 2 and 3 (Figs. 38A, C, D) show a similar but much less marked asymmetry so that the ventral surface faces only slightly laterally. The ungual phalanx of the fourth digit is slightly asymmetrical in the reverse manner (Fig. 38E).

The crushed distal ends of four metatarsals from the right pes of UCMP 82961 are very similar to those of MNA G2 7233 and the best preserved ones are illustrated (Figs. 38K, L). There are several isolated and much flattened phalanges from the talus slope debris that resemble those of the MNA G2 7233. The eight ungual phalanges fall into four sized pairs that closely correspond to those of MNA G2 7233 (cf. Figs. 38B–E, F–I).
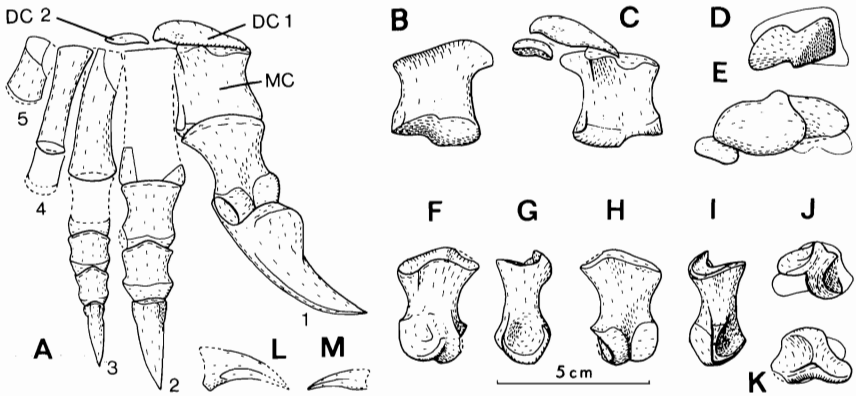
FIG. 36. *Ammosaurus*. UCMP 82961. Left manus × 0.4. *A*, in ventral view; *B*, dorsal view of metacarpal 1; *C*, ventral view of distal carpals and metacarpal 1; *D*, distal end of metacarpal 1; *E*, proximal ends of distal carpals and metacarpal 1; *F–K* phalanx 1 of digit 1 in F, dorsal view; *G*, lateral view; *H*, ventral view; *I*, medial view; *J*, distal view; *K*, proximal view; *L*, ungual phalanx 2 from MNA G2 7233; *M*, ungual phalanx 3 from MNA G2 7233. Abbreviations: *DC* = distal carpal; *MC*, metacarpal.

FIG. 37. *Ammosaurus*. MNA G2 7233. Pubes and hind limb × 0.4. *A*, pubes in dorsal view; *B*, right lower leg as preserved, from a photograph; *C*, left pes as preserved. Abbreviations: *AS* = astragalus; *CA* = calcaneum; *DT* = distal tarsal; *FIB* = fibula; *MT* = metarsal; *TIB* = tibia; *obt for* = obturator foramen.
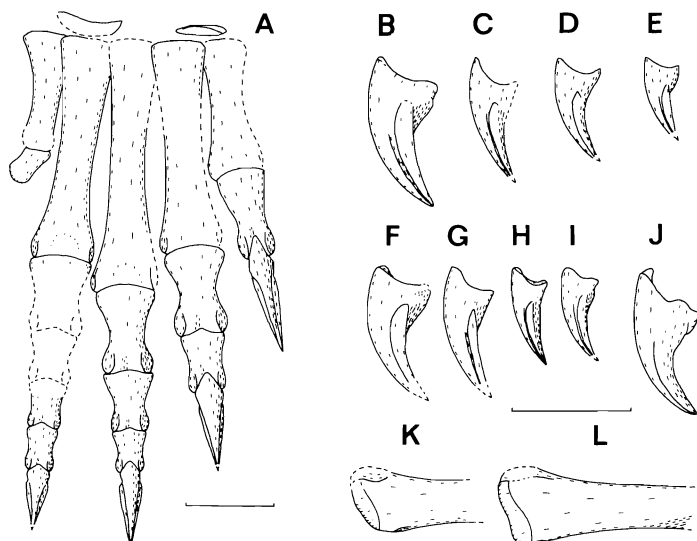
FIG. 38. *Ammosaurus.* × 0.4. *A*, Right pes MNA G2 7233 in dorsal view; *B–E*, ungual phalanges of MNA G2 7233: *B*, ungual 1 from right pes in medial view; *C*, ungual 2 from left pes in lateral view; *D*, ungual 3 from left pes in lateral view; *E*, ungual 4 from left pes in lateral view; *F–I*, ungual phalanges 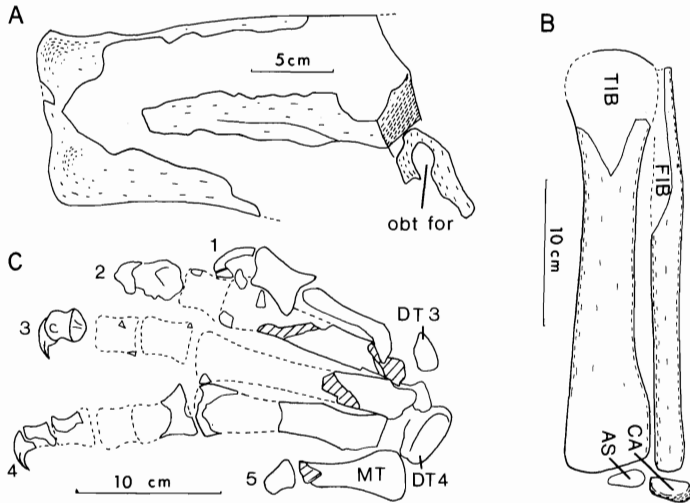of UCMP 82961: *F*, ungual 1 from right pes in medial view; *G*, ungual 2 from right pes in medial view; *H*, ungual 3 from right pes in medial view; *I*, ungual 4 from left pes in lateral view; *J*, ungual 1 from left manus of UCMP 82961 in lateral view; *K–L*, metatarsals of right foot of UCMP 82961 in dorsal view; *K*, metatarsal 1; *L*, metatarsal 2. Scale lines represent 5 cm.

"*Thecodontosaurus*" *gibbidens*
Isolated Teeth

Cope (1878) described as *Thecodontosaurus gibbidens* a few isolated teeth from the black limestone and marl of Upper Triassic age in the Phoenixville Tunnel, York County, Pennsylvania. Two of these teeth were figured by Huene (1921) who regarded them as prosauropod. However, these teeth are almost circular in outline rather than oval in cross section as in prosauropods (*Thecodontosaurus* Riley and Stutchbury 1840, *Anchisaurus* YPM 1883, *Plateosaurus* AMNH 6810). These teeth are provisionally referred to the Ornithischia.

4. TAXONOMY AND SYSTEMATICS

Introduction

Hitchcock (1855, 1858) did not apply a name to the Springfield material (AM 41/109), although it was later named *Megadactylus polyzelus* by Hitchcock, Jr. (1865). Marsh (1882) replaced *Megadactylus* (preoccupied) with *Amphisaurus* and when this also proved to be preoccupied Marsh (1885) substituted the name *Anchisaurus*. Marsh (1882, 1885) made no specimen references, but the generic name *Anchisaurus* could only have referred to Hitchcock's *Megadactylus polyzelus* so, as Lull (1915, 1953) noted, *Anchisaurus (Megadactylus) polyzelus* (Hitchcock, Jr.) is the type species of the genus *Anchisaurus* Marsh. Marsh later erected three new species of *Anchisaurus*: *A. major* (1889, holotype YPM 208), *A. colurus* (1891, holotype YPM 1883) and *A. solus* (1892, holotype YPM 209) but one of these (*A. major*) Marsh (1891) subsequently made the type species of the new genus *Ammosaurus*. Marsh (1885) erected the family Anchisauridae (replaced Amphisauridae of Marsh, 1882) and later (1891, 1895, 1896) he referred *Ammosaurus* to this family.

Huene (1906) noted that *Anchisaurus polyzelus* resembled *A. colurus* in having elongate dorsal vertebrae. However, he considered that *Anchisaurus polyzelus* could be distinguished from *A. colurus* in possessing the following features: narrower neural spines to the anterior caudal vertebrae, a fourth trochanter that was probably higher placed on the femur and a more slender metacarpus. Huene considered that in these respects and in the form of the radius, tibia and fibula *polyzelus* was more similar to the European genus *Thecodontosaurus* Riley and Stutchbury, 1836; so he referred this species to *Thecodontosaurus* as *T. polyzelus*. On the basis of this synonomy Huene (1906) proposed the family name Thecodontosauridae to replace Anchisauridae.

Lull (1915, 1953) objected to the referral of *Anchisaurus polyzelus* to the genus *Thecodontosaurus*. He noted that the caudal vertebrae are not preserved in YPM 1883 and that the tail in the reconstruction published by Marsh (1893, 1895, 1896) was based on YPM 209. Lull considered that the dorsal spines of the anterior caudals of AM 41/109 would have graded into ones similar to those of the preserved caudal vertebra of YPM 209. Lull noted that the proximal end of the femur of YPM 1883 is missing and that the trochanter bearing part of AM 41/109 has no attachment to either end of the femur. Lull (1915) also pointed out that *polyzelus* is the type species of the genus *Anchisaurus*; so, if Huene (1906) was correct, then *Anchisaurus* is a synonym for *Thecodontosaurus* and the species *colurus* and *solus* are left without a genus. Huene (1932) rectified this oversight by referring *Anchisaurus solus* to the genus *Ammosaurus* (as

Ammosaurus solus, see below) and making *Anchisaurus colurus* the type species of the new genus *Yaleosaurus*.

Huene (1932) considered that the principal difference between *Thecodontosaurus polyzelus* and the European *T. antiquus* was the much shorter trunk vertebrae (especially hind dorsal vertebrae) of the American species. He noted that the position of the fourth trochanter of the femur is similar and that the anterior limb of *Thecodontosaurus polyzelus* is relatively very large whereas the hand of *Yaleosaurus* is more slender. Huene (1932) cited his earlier paper (1914b) in which he deduced that the ventral end of the quadrate of *Thecodontosaurus* was more posteriorly directed rather than being anteriorly directed as in *Yaleosaurus*. The features cited were the shortness of the basipterygoid processes, the lower position of the supraoccipital, the more ventrally directed opisthotic and the much deeper basioccipital tuberosity of the braincase of *Yaleosaurus* (Figs. 14 C, D, E) when compared to an isolated braincase referred to *Thecodontosaurus antiquus*. Postcranially *Thecodontosaurus* and *Yaleosaurus* are similar, but Huene (1932) considered that in *Yaleosaurus* the humerus is weaker, the lower arm longer, the tibia shorter, and the metatarsus remarkably longer. Huene concluded that *Yaleosaurus* was better adapted for upright walking than was *Thecodontosaurus*.

Chiefly because of the elongate anterior process of the ilium Huene (1906) referred *Ammosaurus major* to the dinosaurian order Ornithischia, suborder Ornithopoda, family ? Nanosauridae. Upon the receipt of figures of YPM 208 from Lull, Huene (1907–08) revised this conclusion and referred *Ammosaurus* to the family Thecodontosauridae. However, Huene noted that *Ammosaurus* occupied a rather isolated position because of the form of the ilium and ischium and in having a tibia longer than the femur. Later Huene (1914a) erected the family Ammosauridae that he placed adjacent to the family Thecodontosauridae in his classification of the dinosaurs.

Huene (1932) referred *Anchisaurus solus* (YPM 209) to the genus *Ammosaurus* as *A. solus* because of the similarity in the form of the ilium and the elongate nature of the tibia and of the dorsal vertebrae. Huene considered that *Ammosaurus* (YPM 208, 209) differed from the thecodontosaurids in possessing the following features:
1) a large skull with a carnivorous dentition;
2) a low presacral vertebral count of 23;
3) amazingly slender and elongate vertebrae even in the back;
4) an elongate anterior process to the ilium;
5) tibia longer than femur.
Huene considered that *Ammosaurus* could be separated from all other Triassic genera by features 1, 4, 5, and, in addition, by the extreme hollowness and delicateness of all the bones, and by the unusual form of the pubis and ischium. Huene concluded that *Ammosaurus* was not a prosauropod

(herbivorous group including the Thecodontosauridae) and, on the basis of features 2, 5, and the hollowness of the bones, he referred this genus to the Coelurosauria (carnivorous, bipedal, fast-running theropods). Huene (1932, 1956) considered that because of the unusually slender presacral vertebrae, the relatively short sacrum and the unspecialized metatarsus *Ammosaurus* still often walked quadrupedally and that the Ammosauridae was the most primitive family of coelurosaurs. Lull (1953) accepted that *Ammosaurus major* was a primitive coelurosaur and that *Yaleosaurus* was a valid genus. However, Lull still recognized two species of *Anchisaurus, A. polyzelus* and *A. solus.*

From the above review it is apparent that there are several taxonomic problems; these will be discussed in the following sections which will substantiate the conclusions that I presented elsewhere (Galton, 1971a). (See above: Table 1).

Validity of *Anchisaurus* Marsh

As mentioned above Huene (1906, 1932) made *Anchisaurus* Marsh a synonym of the European genus *Thecodontosaurus* Riley and Stutchbury. Riley and Stutchbury (1836) described and subsequently (1840) figured various dinosaurian bones from the Magnesian Conglomerate (Rhaetic, Upper Triassic) from Durdham Down near Bristol, England. They designated an incomplete dentary with teeth (see Riley and Stutchbury, 1840, pl. 29, fig. 1) as representing a new genus *Thecodontosaurus*, but they did not provide a specific name; this omission was rectified by Morris (1843:211) who erected the species *T. antiquus.* Riley and Stutchbury (1836) also designated an isolated tooth (see Riley and Stutchbury, 1840, pl. 29, fig. 4) as *Palaeosaurus cylindrodon.* Riley and Stutchbury (1840) made no attempt to divide the bones they described between the two genera, but this was done by Seeley (1895a) and Huene (1907–08, list: 215–216; *T. cylindrodon* later recognized as *P. cylindrodon* by Huene, 1914a, 1932), both of whom described additional material. However, to my knowledge the only naturally articulated bones of *Thecodontosaurus* described from Bristol are a few short series of vertebrae (Huene, 1907–08, figs. 214, 218, 220; 1914b, fig. 39) and an articulated scapula and forelimb (Huene, 1914b, fig. 46; Galton and Cluver, in press, figs. 11A–G). Most of the bones are disarticulated and there is no undoubtedly natural articulated association of bones with either type of teeth. Consequently any attempt to reconstruct the anatomy of *Thecodontosaurus* or *Palaeosaurus* is rather speculative and very arbitrary. These genera proposed by Riley and Stutchbury (1836) are tooth genera that at the moment cannot be applied to skeletal material.

The holotype of *Anchisaurus polyzelus* (AM 41/109) does not include any skull material and the teeth of the other specimen (YPM 1883) are not well enough preserved for any meaningful comparisons to be made with those of *Thecodontosaurus*. I consider that *Anchisaurus* is a valid genus and, as summarized in the generic diagnoses (p. 88, p. 89), *Anchisaurus* can be distinguished from the material referred to *Thecodontosaurus* by various anatomical differences, some of which are discussed in the next section in considering the validity of the genus *Yaleosaurus*.

Taxonomic Status of YPM 1833

Marsh (1891) made YPM 1883 the holotype of a new species of *Anchisaurus*, *A. colurus*, but he did not indicate how it differed from *A. polyzelus* (AM 41/109). Huene (1906) suggested that *Anchisaurus polyzelus* resembled *Thecodontosaurus* and differed from *Anchisaurus colurus* in several features that will be discussed with others noted later by Huene (1907–08, 1932).
1. Shortness of cervical vertebrae. Huene (1932) noted that AM 41/109 resembled *Thecodontosaurus* in the shortness of the anterior cervical vertebrae that in YPM 1883 are elongate (Figs. 15C–F). However, this comparison was based on the misidentification of part of the neural arch of a sacral vertebra (Figs. 3E–G) as a cervical vertebra (Huene, 1914b, fig. 23a).
2. Shortness of dorsal vertebrae. Huene (1906) originally noted that AM 41/109 differed from *Thecodontosaurus* and resembled YPM 1883 in having very elongate dorsal vertebrae. Later Huene (1914b) figured an extremely short centrum of AM 41/109 as that of a dorsal vertebrae. Although not stated this implies that the dorsal vertebrae of AM 41/109 are extremely short in comparison with those of YPM 1883. The isolated centrum figured by Huene (1914b) could not be located, but from the proportions it was probably part of an anterior caudal vertebra. The proportions of the isolated neural arch (Figs. 3A–C) and of the centrum (Fig. 5C) show that the dorsal vertebrae of AM 41/109 were probably elongate (or rather the centra were low) as in YPM 1883 (Figs. 15I, J). However, the centrum of the last dorsal vertebra of YPM 1883 is elongate (Fig. 15L) in comparison with that of AM 41/109 (Figs. 5F–J) if, as appears to be the case, this isolated centrum is correctly identified (it might be sacral 3 but it is similar to the last dorsal of *Efraasia*, Galton, 1973a). Taking the length of AM 41/109 as unity the ratio of the lengths of the centra of dorsal vertebra 15 of AM 41/109 and YPM 1883 is 1:1.45 as against 1:1.25 for the lengths of metatarsal 2 (or 4) and the length of the femur. However, this difference might be an individual or sexual difference.

3. Slenderness of neural spines of anterior caudal vertebrae. This com-
parison by Huene (1906) was based on misleading figures given by Cope
(1870) and Marsh (1893, 1895, 1896). Cope (1870, pl. 8, fig. 7; see Lull,
1953, fig. 12a) did not indicate that the neural spines of the anterior caudal
vertebrae of AM 41/109 were damaged and incomplete (Fig. 5L); orig-
inally the neural spines were broader and not so narrow as in the ver-
tebrae referred to *Thecodontosaurus* (see Huene, 1907–08, pl. 77, fig. 4;
1914b, fig. 40). The tail of YPM 1883 is not preserved and this region
was restored by Marsh (1893, 1895, 1896) from YPM 209 (Fig. 30B)
that I refer to *Ammosaurus* (see below).
4. Form of radius. Only the distal end of the radius of AM 41/109 is
preserved (Fig. 7A), but it is very similar to that of YPM 1883 (Fig. 17C).
5. Slenderness of metacarpals and phalanges. Despite differences in pres-
ervation the manus of AM 41/109 (Figs. 7A, L) and YPM 1883 (Figs.
17C, 18) are almost identical and both are slender in comparison with the
manus of all other prosauropods except *Thecodontosaurus* and *Efraasia*
(Galton, 1971a, 1973a). The ungual phalanx of digit 1 is more trenchant
in AM 41/109 (Figs. 7I, L) than it is in YPM 1883 (Figs. 17C, D, 18),
but this is probably an individual or sexual difference (with AM 41/109
as male).
6. Proportionally larger size of forelimb. Huene (1932:121) admitted
that the lengths of the humerus, radius, and tibia were restored for AM
41/109 and that the lengths of the femora of both specimens were estimated.
In addition, it should be noted that the tibia of YPM 1883 was much
shortened by compression during preservation. Consequently it is almost
impossible to compare the relative sizes of the forelimbs of AM 41/109
and YPM 1883. However, taking AM 41/109 as unity the ratio of the
lengths of metacarpal 2 of AM 41/109 and YPM 1883 is 1:1.44 as
against 1:1.25 for the lengths of metatarsal 2 (or 4) and of the femur.
Nopcsa (1929) regarded a similar difference in the size of the manus of
the ornithopod *Iguanodon mantelli* as a sexual dimorphism.
7. Proportionally higher position of the fourth trochanter of femur. Lull
(1915, 1953) considered that the relative position of this trochanter in
the two femora was a matter of conjecture, but Cope (1870), Huene
(1914b) and Lull (1915, 1953) only figured three of the four pieces of the
femur of AM 41/109. The curves of the four pieces can be matched to
give a reasonably accurate reconstruction of the femur (Fig. 8). The
femur of YPM 1883 (Fig. 21) lacks only a small part of the head, prob-
ably about 10 mm. Taking AM 41/109 as unity, the ratio of the lengths
of the femora of AM 41/109 and YPM 1883 is 1:1.25 as is also the ratio
of the distance from the proximal end of femur to the base of the fourth
trochanter.
8. Form of tibia and fibula. Only the proximal end of the tibia of AM
41/109 is preserved and it has been laterally compressed whereas the tibia

of YPM 1883 has been longitudinally compressed (Figs. 22A, B, D). I consider that the slight differences in the form of these tibiae are the result of differences in preservation and that the same is also true for the fibulae.

It is apparent that the differences between AM 41/109 and YPM 1883 are minimal and can be attributed either to differences in preservation or to individual variation, a factor that tends to be overlooked. Individuals of the ornithopod dinosaur *Hypsilophodon foxii* show a much wider range of morphological variation (see Galton, 1974) than that discussed above. I conclude that YPM 1883 should be referred to *Anchisaurus polyzelus* because, on the basis of the available material, YPM 1883 cannot be distinguished from AM 41/109 by any characters of taxonomic significance and, in addition, AM 41/109 does not show any unique resemblance to *Thecodontosaurus*. Consequently *Anchisaurus colurus* Marsh is a junior synonym of *Anchisaurus polyzelus* (Hitchcock, Jr.) and *Yaleosaurus* Huene is a synonym for *Anchisaurus* Marsh (for diagnosis see p. 88).

Validity of *Ammosaurus* Marsh

Since Marsh (1891) made *Anchisaurus major* Marsh, 1889 the type species of the new genus *Ammosaurus* the validity of this genus has never been questioned. Unlike *Anchisaurus, Ammosaurus* has a broad hind foot (Fig. 15D) as do most other prosauropods. On the basis of the holotype (YPM 208) *Ammosaurus* is characterized as a broad-footed prosauropod with the following combination of characters: centra of dorsal vertebrae low, no contact between distal parts of transverse process and sacral rib of third sacral vertebra, elongate anterior process to ilium, subacetabular part of ischium emarginated ventrally.

Taxonomic Status of YPM 209

Marsh (1892) made YPM 209 the holotype of a new species of *Anchisaurus, A. solus*, but he did not figure the specimen, define the species or give any reasons why it should be referred to *Anchisaurus* rather than to *Ammosaurus*. Huene (1906) questioned the assignment of YPM 209 to *Anchisaurus*, accepted it (1914b), and subsequently (1932) referred it to *Ammosaurus* as *Ammosaurus solus*. In support of this referral Huene (1932) cited the similarities of the ilium and of the dorsal vertebrae of *Ammosaurus* and YPM 209 plus the possession of a tibia that was longer than the femur. However, a preparation of the ilium of *Anchisaurus* (Fig. 19A) shows that it is very similar to that of *Ammosaurus* (Fig. 26E) and the ilium of YPM 209 (Fig. 31E) is too incomplete for any comparisons

to be made with either. The posterior dorsal vertebrae are low in both *Anchisaurus* (Figs. 15H–J) and *Ammosaurus*. The tibia of both YPM 208 and YPM 209 was probably shorter than the femur (see descriptions of specimens) as is also the case for *Anchisaurus*. Consequently the generic position of YPM 209 cannot be determined by these characters, but the metatarsus of YPM 209 (Figs. 30B, 31F) appears to be broad as in *Ammosaurus* (Figs. 28, 29D) rather than slender as in *Anchisaurus* (Figs. 12, 22E). I therefore agree with Huene (1932) in referring YPM 209 to the genus *Ammosaurus*. However, apart from the difference in size (estimated total length of YPM 208 about 3 m, 209 about 1 m) there are no diagnostic characters by which the two specimens can be distinguished. The incomplete ossification of the bones (especially vertebrae) show that YPM 209 represents a young animal. I regard YPM 209 as a juvenile *Ammosaurus major*; so *Anchisaurus solus* Marsh and *Ammosaurus solus* (Marsh) are junior synonyms of *Ammosaurus major* (Marsh).

Taxonomic Status of Specimens from Arizona

The ungual phalanges of the pes of UCMP 82961 (Figs. 38F–H) are very similar to those of MNA G2 7233 (Figs. 38B–E) and the form of the manus (Figs. 35A, 36A) is characteristically prosauropod. Brady (1935) noted that the pes of MNA G2 7233 resembled that of *Ammosaurus major* as figured by Marsh (1896) (see Figs. 28, 29A, 35B, 38A). In both the foot is broad and stout with an expanded distal end to metatarsals 1 to 4 and the ungual phalanx of the first digit is the largest. There are differences between the relative proportions of the metatarsals and phalanges of the feet of MNA G2 7233 and *Ammosaurus major*. However, both specimens are crushed and damaged, with these proportions differing on opposite sides of the animal (Table 3); so it is reasonable to refer the specimens from Arizona to the genus *Ammosaurus*. The specimens may represent a new species and one difference is that the obturator foramen of the pubis (Fig. 37A) appears to be smaller than in *Ammosaurus major* (Figs. 26E, F). However, bearing in mind the incompleteness of the three specimens concerned, I consider it inadvisable to erect a new species on the basis of the material available. Consequently I refer both specimens to *Ammosaurus* as *A*. cf. *major*.

Family Ammosauridae

Huene (1907–08) noted that *Ammosaurus* occupied a rather isolated position with respect to the other thecodontosaurids and later (1914a) erected the family Ammosauridae in a bibliography of the literature on

dinosaurs. Subsequently Huene (1932) listed several features in which *Ammosaurus* (YPM 208, 209) differed from the thecodontosaurids and these will be discussed as follows:

1. Skull large with a carnivorous dentition. The mandible of YPM 209 is almost complete (Fig. 31A) and the ratio of its length to that of the presacral vertebrae is 0.137 as against 0.134 for *Plateosaurus* (calculated from Huene, 1926, pl. 7) and 0.23 for the coelurosaur *Coelophysis* (calculated from Colbert, 1961, fig. 8); so the size of the skull of YPM 209 is much more comparable to that of prosauropods. The teeth of YPM 209 (Fig. 31B) are not well preserved, but they are similar to those of *Anchisaurus* (Figs. 13B, 14A) and *Plateosaurus* (AMNH 6810).

2. Low presacral count of 23 vertebrae. Huene (1906, 1914b, 1932, 1956) thought that YPM 209 had 9 cervical and 14 dorsal vertebrae, one of which was hidden by the matrix supporting the apron region of the pubis. However, 10 cervicals are visible and there were probably 15 dorsals because there is room for two dorsal vertebrae in the matrix below the pubes (Figs. 30A, 31D). (See p. 60.)

3. Extremely slender and elongate vertebrae. The vertebrae are best exposed in YPM 209 (Fig. 30A), but it is difficult to understand why Huene cited this feature because the vertebrae (centra) of *Anchisaurus* (Figs. 15J, L) are equally slender and elongate.

4. Elongate anterior process to the ilium. This was a unique feature when Huene (1906, 1907–08, 1932) considered the problem. However, exposure of the lateral surface of the ilium of *Anchisaurus* shows that it also has an elongate anterior process (Fig. 19A) and, in addition, it appears that the anterior process of *A. capensis* (Broom, 1906, Galton and Cluver, in press) was also long.

5. Tibia longer than femur. Examination of the specimens shows that the femur was definitely longer than the tibia in YPM 208 and that this was probably also the case for YPM 209 (see p. 57, p. 66.)

It is apparent that *Ammosaurus* cannot be distinguished from all other Triassic genera on the basis of features 1, 4, and 5 as suggested by Huene (1932) and this is also true for the additional features cited. The bones of *Ammosaurus* (YPM 208) are no more hollow and delicate than are those of *Anchisaurus*. The pubis of *Ammosaurus* (Figs. 26E, F) is not unique and it is similar to that of most other prosauropods such as *Efraasia* (Figs. 20D, E) and *Plateosaurus* (Huene, 1926, 1932). The ischium is unusual in the ventral emargination of the subacetabular region (Figs. 20D, E), but the pubis of *Anchisaurus* (Figs. 19A, 20A, C) shows a comparable emargination.

Prosauropod Characters of *Ammosaurus*

Colbert (1964b) and Charig et al. (1965) have considered the character-istic features of prosauropods and the following discussion is modified from my earlier summary of the prosauropod characters of *Ammosaurus* (Galton, 1971a). The specimen concerned is indicated in parentheses and the characters are listed in Table 5 with an indication of the occurrence of each in the four specimens of *Ammosaurus, Anchisaurus, Plateosaurus* and *Efraasia*.

As noted above there appear to have been 25 presacral vertebrae in YPM 209 (Figs. 2B, 30A), a count typical of prosauropods and in contrast to the 23 or 24 of theropods (see Charig et al., 1965), the third sacral vertebra is clearly a modified caudal vertebra (YPM 208, Fig. 26E). The manus of YPM 209 (Fig. 31C) is very poorly preserved, but that of UCMP 82961 (Figs. 35A, 36A) is clearly that of a prosauropod.

The pelvic girdle of both specimens is the brachyiliac type characteristic of prosauropods; so the ilium and pubis are rather different from those of the dolichoiliac type characteristic of theropods (Fig. 39; see Colbert, 1964b). The pubic peduncle of the ilium is broad and is much longer than the ischiadic head; so the acetabulum is large with an elliptical outline (Figs. 26E, 31E, 39A; YPM 208, 209), rather than small with an oval outline as in theropods (Figs. 39B, C). The size of the anterior process of the ilium cannot be determined in YPM 209, but that of YPM 208 is long (Fig. 26E). As a result the ratio of the length of the ilium to its height at the ischiadic head is about 2.0 in YPM 208 as against 1.3 in *Plate-osaurus* (Fig. 39A) and 2.5 in *Coelophysis* (Fig. 39C). The anterior process of YPM 208 is rather different from the small triangle that Colbert (1964b) and Charig et al. (1965) considered characteristic of prosauropods. However, the process is slender and it is not the deep plate so character-istic of theropods (Figs. 39B, C). The anterior process is also elongate in the prosauropods *Anchisaurus polyzelus* (Fig. 19A) and *A. capensis* (Broom, 1906; Galton and Cluver, in press).

The distal part of the pubis forms a broad, transversely oriented apron (Figs. 26F, 31D), but more proximally the bones are twisted (YPM 208, 209). Ventral to the acetabular region there is a deep plate with a large obturator foramen (Figs. 26E, F; this region not preserved in YPM 209). These features are characteristic of prosauropods (Fig. 39A) and are in marked contrast to the straight, rodlike pubis of theropods (Figs. 39B, C) in which there is usually only a small plate ventral to the acetabulum and no obturator foramen [a *small* obturator foramen has been reported in only *Ceratosaurus* (see Gilmore, 1920, pl. 23) and *Syntarsus* (see Raath, 1969, Fig. 4B)]. The proximal part of the ischium of YPM 208 (Figs. 26E, F) is not typically prosauropod because, ventral to the acetabulum, it is not platelike but is quite shallow so that there is a relatively short union with

TABLE 5. Prosauropod Characters of *Ammosaurus*.

Character	A	B	C	D	E	F	G
1) Teeth spatulate.	+	+			+		+
2) Twenty-five presacral vertebrae.		+				+	+
3) Third sacral from caudal series.	+				+		+
4) Enormous pollex on manus.		–		+	+	+	+
5) Long pubic peduncle to ilium, elliptical acetabulum.	+	+			+	+	+
6) Small triangular anterior process to ilium.	×				×	+	+
7) Proximal part of pubis deep, large obturator foramen.	+		–		×	+	+
8) Pubis twisted with broad apron distally.	+	+	+		×	+	+
9) Proximal part of ischium deep.	×						+
10) Small lesser trochanter to femur.	+		+		+	+	+
11) Tibia shorter than femur.	+	–	+		+	+	+
12) Central ascending process of astragalus keying into tibia.	–				+	+	+
13) Pes broad and distal end of metatarsals expanded.	+	+	+	+	×	×	+
14) Metatarsal 1 complete, digit anteriorly directed.	+	+	+		+	+	+
15) First ungual phalanx largest on pes.	+		+	+	×	+	+
16) Digit 3 not elongated relative to digits 2 and 4.	+		+		+	+	+
17) Metatarsal 5 quite large.			+		+	+	
18) Phalanx on metatarsal 5.	+	+					+

Abbreviations: A–D, *Ammosaurus*: A = YPM 208; B = YPM 209; C = MNA G2 7233; D = UCMP 82961; E = *Anchisaurus*, YPM 1883; F = *Efraasia*, SMNS 12667, 12668; G = *Plateosaurus* (see Huene, 1926). + = yes; – = possibly so; × = no; no entry indicates that this region is not known.

the pubis. There are indications of an obturator process and the ischium is rather theropodlike (Fig. 39B). However, this is a convergent feature resulting from the emargination of the anteroventral part of an ordinary prosauropod ischium (Fig. 39A) and the pubis of *Anchisaurus* (Figs. 19A, 20A, C) shows a comparable emargination.

The femur lacks the prominent lesser trochanter (YPM 208, Fig. 27A) so characteristic of theropods, and it is longer than the· tibia on both YPM 208 and 209 (see above). Charig et al. (1965) pointed out that the astragalus of prosauropods has a central ascending process that keys into the distal end of the tibia that backs the astragalus with a descending flange. There are indications of such a central ascending process on the astragalus of YPM 208. In theropods the anterior process fits against the anterior surface of the tibia. However, the structure of the ankle is not so diagnostic as Charig et al. (1965) thought because the coelurosaur *Syntarsus* from the
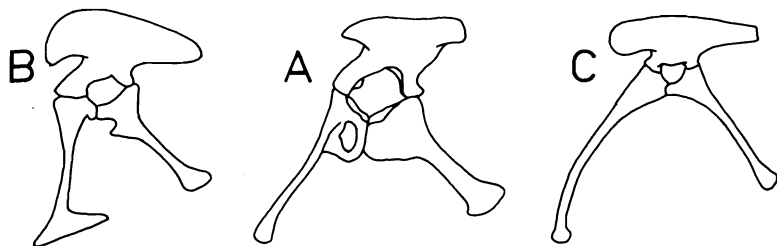
FIG. 39. Pelvic girdles of saurischian dinosaurs in lateral view, not drawn to same scale. *A*, brachyiliac type, the prosauropod *Plateosaurus*, after Huene (1926); *B*, dolichoilic type, the carnosaurian theropod *Allosaurus*, after Gilmore (1920); *C*. dolichoilic type, the coelurosaurian theropod *Coelophysis*, after Colbert (1964b).

Late Triassic of Rhodesia has a typically "sauropodomorph" tibia and astra-galus (see Raath, 1969, fig. 6). The structure of the pes (Figs. 28, 29D) is that of typical prosauropods, being broad with a shortened but complete first metatarsal (YPM 208, 209). In theropods the first metatarsal is long but slender with the proximal section of the shaft unossified. The ungual pha-lanx of the first digit is the largest (YPM 208), and it is anteriorly directed (YPM 208, 209) rather than posteriorly directed as in some theropods.

I conclude that *Ammosaurus* is a prosauropod dinosaur with a few specialized features (long anterior process to ilium, emarginated subace-tabular part of ischium, form of third sacral rib) that do not justify the retention of a separate family for this genus.

Families Anchisauridae and Plateosauridae

The infraorder Prosauropoda is currently divided into three families: An-chisauridae (= Thecodontosauridae), Plateosauridae and Melanorosauri-dae (see Romer, 1956; Colbert, 1964b; Charig et al. 1965; Bonaparte, 1972; for generic lists see Romer, 1966:370). The separation is clearest between melanorosaurids and nonmelanorosaurids (see Romer, 1956:617–8; Bona-parte, 1972:160–1). Elsewhere (Galton, 1971a, 1973a) I suggest that the range of morphological variation is insufficient to warrant the retention of two families of nonmelanorosaurid prosauropods. This suggestion was based on postcranial anatomy but, upon reflection, genera with skulls as different as those of *Anchisaurus* (Figs. 14A, B) and *Plateosaurus* (Figs. 14I, J) should not be included in the same family. Consequently they are referred to the families Anchisauridae (Marsh, 1885) and Plateosauridae (Marsh, 1895), the first two valid prosauropod family names to be pro-

posed. Unfortunately most of the genera currently referred to the family Anchisauridae lack cranial material, but, as noted by Galton (1971a, 1973a), only four genera (*Anchisaurus, Efraasia, Gyposaurus, Thecodontosaurus*) are slender-footed. I now provisionally restrict the family Anchisauridae to *Anchisaurus, Efraasia* and *Thecodontosaurus* and refer the broad-footed anchisaurids plus *Ammosaurus* to the family Plateosauridae. A full discussion of this revision will be presented elsewhere (Galton and Cluver, in press) and is summarized below.

<div align="center">

SYSTEMATICS
ORDER Saurischia
SUBORDER Sauropodomorpha
INFRAORDER Prosauropoda

</div>

<div align="center">

FAMILY Anchisauridae Marsh, 1885:169

</div>

Smaller forms, skull lightly built, shallow posterior half of lower jaw with articulation in line with tooth row, manus and pes slender.

Anchisaurus Marsh, 1885:169 (*Amphisaurus, Gyposaurus, Megadactylus, Yaleosaurus*). About 9 maxillary teeth, 16 dentary teeth, basipterygoid processes very small, cervical vertebrae elongate, centra of dorsal vertebrae low, broad bases to neural spines of anterior caudal vertebrae, metacarpal 1 broad, digits 1 and 2 of manus subequal in length, ilium with a long anterior process, pubis with an open obturator foramen, and a relatively narrow distal part that is not apronlike.

A. polyzelus (Hitchcock, Jr., 1865:40) (*A. coelurus*). Ungual 1 of pes smaller than ungual 3.

A. capensis (Broom, 1911:293). Ungual 1 largest on pes. It should be noted that "*Gyposaurus*" *sinensis* Young, 1941 from China is a broad-footed prosauropod incorrectly referred to the genus *Gyposaurus;* the species *sinensis* is based on juvenile individuals of *Lufengosaurus huenei* Young (see Rozhdestvenskii, 1966; Galton and Cluver, in press).

Efraasia Galton, 1973a:247, *E. diagnostica* (Huene, 1932:73) (Fig. 1A). Basipterygoid processes of medium length, cervical vertebrae elongate, centra of dorsal vertebrae low, narrow bases to neural spines of anterior caudal vertebrae, slender metacarpal 1, digit 2 of the manus robust and noticeably longer than 3, ilium with a short triangular anterior process, pubis with a closed obturator foramen and an apronlike distal part, ungual 1 largest on the pes. *Efraasia* is a good ancestor for *Anchisaurus* (see Galton, 1973a).

Thecodontosaurus Riley and Stutchbury, 1836:349, *T. antiquus* Morris, 1843:211. At least 21 dentary teeth (in holotype), from referred specimens (not found in articulated association with *Thecodontosaurus* teeth) diagnosis tentatively expanded as follows: elongate basipterygoid processes,

short cervical vertebrae, high centra to dorsal vertebrae, narrow base to neural spines of anterior caudal vertebrae, high placed deltopectoral crest on proximal third of humerus, manus with a slender metacarpal 1, and digits 2 and 3 subequal in length, short triangular anterior process to ilium.

   Incertae sedis. Thecodontosaurus (Hortalotarsus) skirtopodus (Seeley, 1894:411), *T. (Agrosaurus) macgillivrayvi* (Seeley, 1891: 161) and *T. (Massospondylus) browni* (Seeley, 1895b:118) of Huene (1906:145) plus *T. minor* Haughton (1918:468) all represent anchisaurids, but the specimens upon which these taxa are based are generically and specifically indeterminate (Galton and Cluver, in press).

<div align="center">FAMILY Plateosauridae Marsh, 1895</div>

Larger forms, skull massively built, deep posterior half to lower jaw with articulation offset ventral to line of tooth row, manus and pes broad.

   The following taxa are referred to this family:
Ammosaurus (for diagnosis see p. 83 - 84), *Aristosaurus, Lufengosaurus* ("*Gyposaurus*" *sinensis, Yunnanosaurus), Massospondylus (Aetonyx, Dromicosaurus, Gryponyx, Leptospondylus, Pachyspondylus), Plateosaurus (Dimodosaurus, Gresslyosaurus, Pachysaurus, Platysaurus, Sellosaurus).*

<div align="center">5. BIOLOGY OF PROSAUROPODS</div>

<div align="center">The Skull of Prosauropods</div>

Charig et al. (1965) have suggested that the large recurved carnosaurlike teeth and the supposedly associated postcranial material described by Young (1951) as *Sinosaurus* represents a carnivorous melanorosaurid prosauropod, but, apart from this, the prosauropods appear to have been herbivorous. However, in certain cases such as *Anchisaurus* (Fig. 14A), *Massospondylus* (Charig et al., 1965) and *Plateosaurus* (Huene, 1926, pl. 1, figs. 1, 2 — premaxillary teeth; AMNH 6810) the anterior teeth are slightly recurved whereas further back they are of the spatulate type normal for prosauropods. The skull of *Anchisaurus* (Figs. 14A, B) is lightly built, but in the larger forms such as *Plateosaurus* (Figs. 14I, J) and *Lufengosaurus* (Young, 1951) it is much more heavily built with a ventrally offset jaw articulation. In herbivorous mammals this articulation is offset dorsally, but the system is functionally analagous; it increases the angle between the muscle lever arm and the plane of the teeth (Crompton and Hiiemäe, 1969) and this is important when dealing with resistant plant material. In *Plateosaurus* (AMNH 6810) the teeth are straight in anterior view and there are no signs of any wear surfaces on the crowns and, as far as I can

determine, this is the case for all prosauropod teeth. Prosauropods probably could not chew very resistant plant material, but the action of the teeth may have been supplemented by the grinding action of stones in a muscular gastric mill. In the alligatorine *Caiman,* ingested mice are ripped and crushed by stones embedded in the muscular stomach wall (Bakker, 1971). Concentrated masses of small stones ("gizzard stones") have been found inside the rib cages of several saurischian dinosaurs including a sauropod and these finds could represent gastric mills (Bakker, 1971). A well-preserved gastric mill has been found in a specimen of *Massospondylus* (Mr. J. Attridge, personal communication). However, even with the help of a gastric mill prosauropods were probably not very efficient herbivores when compared with the ornithischians that replaced them.

Prosauropod dinosaurs were the dominant large (up to 10 m) terrestrial herbivores towards the end of the Triassic (Norian and Rhaetic periods) and their remains are reported from all continents except Antarctica. Rich terrestrial faunas from these periods are known from Germany (Huene, 1907–08, 1932), South Africa (Haughton, 1924; Huene, 1932), South America (Bonaparte, 1972) and China (Young, 1951). The dominant position of prosauropods is especially marked since Charig et al. (1965) pointed out that most of the postcranial material thought to represent Triassic carnosaurs is actually prosauropod. Terrestrial faunas of early Jurassic age are rare with prosauropods (see p. 7), sauropods and ornithischians represented (Colbert, 1961, 1965). Middle Jurassic terrestrial faunas are also rare with sauropods and ornithischians but no prosauropods (Colbert, 1961, 1965). Terrestrial faunas of late Jurassic age are very well represented by those of the Morrison Formation of North America and the Tendaguru Formation of Tanzania; in both cases there are numerous sauropods and ornithischians, but no sign of any prosauropods (see Colbert, 1961, 1965). Prosauropods were undoubtedly extinct by the late Jurassic and were probably also extinct by the middle Jurassic.

I believe that part of the reason for the elimination of the prosauropods was the relative inefficiency of the masticatory aparatus with respect to that of most ornithischians (Galton, 1972, 1973b; Bakker and Galton, 1974). The tooth rows of the maxillary and dentary of prosauropods are marginal in position (Figs. 14A, D, I, J) as in living reptiles. Prosauropods probably resembled living reptiles in lacking cheeks and in not chewing their food. However, in most ornithischians the maxillary and dentary teeth have well-developed planar wear surfaces so that the teeth were self-sharpened by differential wear. The maxillary and dentary tooth rows of most ornithischians are not marginal in position but are inset with a space lateral to them which is roofed by the overhanging maxilla and floored by the massive dentary. I conclude that this space was bounded laterally by a cheek that prevented the loss of food from the sides of the tooth rows and, as a result, resistant plant material could be reduced to small pieces by repeated

chewing (Galton, 1972, 1973b). In these respects the masticatory apparatus of ornithischians resembled that of mammals much more closely than that of living reptiles. I believe that the increased efficiency of the masticatory apparatus of ornithischians for dealing with resistant plant material was an important reason why this group replaced the prosauropods as the dominant "small- to medium-sized" (up to 10 m) terrestrial herbivores. The locomotary advances of ornithischians were also important (Bakker and Galton, 1974).

    In contrast to the marked uniformity of prosauropods with only three families, ornithischians radiated into four very distinctive suborders with a dozen families (Ornithopoda, 6; Ankylosauria, 2; Stegosauria, 2; Ceratopsia, 2; Romer, 1966). The sauropod dinosaurs with two families continued through Jurassic and Cretaceous times and very successfully fulfilled the role of large terrestrial herbivores (up to 30 m in length; see Bakker, 1971).

                        Quadrupedality of Prosauropods

A habitual biped has hind limbs that are long relative to both the forelimbs and the trunk. In prosauropods the forelimbs are about half the length of the hind limbs, but the trunk is about the same length as the hind limbs (Figs. 1, 2). Taking the length of the complete series of dorsal vertebrae as an approximation of the trunk length and the length of the hind limb as the combined lengths of the femur, tibia, and metatarsal 3, then the hind limb to trunk ratios of certain prosauropods are as follows: *Ammosaurus* 0.94 (Fig. 2A), *Anchisaurus* 0.90 (Fig. 1B), *Aristosaurus* 0.90 (Huene, 1932), *Efraasia* 0.93 (Fig. 1A), *"Gyposaurus" sinensis* 0.96 (Young, 1941), *Massospondylus harriesi* 1.09 (Huene, 1932) and *Plateosaurus* 0.98 (Fig. 2B). These values ranging from 0.90 to 1.09 (some of values given in Galton, 1971a, were trunk to hind limb) are lower than those of truly bipedal dinosaurs (e.g., hadrosaurs 1.22 to 1.44, *Iguanodon* 1.35, *Gorgosaurus* 1.37, *Struthiomimus* 1.9; see Galton, 1970b, table 1), but higher than those of undoubtedly quadrupedal dinosaurs (e.g., *Ankylosaurus* and *Scolosaurus* 0.69, *Stegosaurus* 0.9, *Kentrurosaurus* 0.86, *Triceratops* 0.9, *Apatosaurus* 0.85; see Galton, 1970b, table 2). It should be noted that the hind limb to trunk ratio does not take into account the proportionally elongate neck of prosauropods (Figs. 1, 2). Consequently it is reasonable to presume that prosauropods were only facultatively bipedal, i.e., they were quadrupedal for most of the time, but were occasionally bipedal (Galton, 1971a). Indeed it is interesting to note that the more lightly built and supposedly more bipedal prosauropods such as *Anchisaurus* (Fig. 1B) and *Efraasia* (Fig. 1A) have a lower hind limb-to-trunk ratio than *Plateosaurus* (Fig. 2B).

    I have suggested that the constancy of structure of the prosauropod manus

was correlated with the development of an enormous and trenchant first ungual phalanx that was used while bipedal for offense or defense, in a group 'that was only facultatively bipedal (Galton, 1971a, b). With the first digit in full extension the ungual would have been a formidable weapon; it is larger than the first ungual of the pes (Figs. 38F, J). During quadrupedal locomotion with the digits of the manus in full extension the weight was taken by digits 2 to 4 (mostly 2 and 3), and the enormous first ungual phalanx was held clear of the ground. The lateral surface of this phalanx would only have touched the ground if it was irregular or soft and even then the point of the claw would not have been damaged.

Bipedality became fully developed in theropod dinosaurs, ornithopod dinosaurs, and birds, but the sauropodomorphs (prosauropods, sauropods) remained basically quadrupedal. Carnivorous animals have a relatively short alimentary canal so the trunk of theropods could be shortened so locomotion was completely bipedal without the efficiency of the digestive system being adversely affected. Herbivorous animals have a very long alimentary canal for the proper digestion of plant material, so that in prosauropods a shortened trunk would have restricted the space available for the viscera. Ornithopods were herbivorous and bipedal, but the pubis was reoriented to lie alongside the ischium and, because the prepubic processes were divergent, the viscera were slung below the pelvic girdle. Consequently, the center of gravity was more posteriorly placed and there was enough room for elongate viscera even though the trunk was shortened (Galton, 1969, 1970a). Birds combined the bipedal adaptations of theropods and ornithopods because early birds were carnivorous (insectivorous) and the pubis perhaps lay alongside the ischium.

The anteroventrally directed pubis of most reptiles is the area of origin of the anterior part of the M. puboischio-femoralis externus that is a very important femoral protractor. However, in the ancestors of ornithischian dinosaurs and in birds this muscle was functionally replaced by the differentiation of a large M. iliotibialis 1 which originated from the enlarged anterior process of the ilium. Once the muscles of the pubis were no longer essential for femoral protraction then the balance problems of full bipedality could be solved by rotating the pubis posteriorly, so that the viscera were slung between the hind limbs (Galton, 1969, 1970a).

I consider that the sauropodomorphs remained basically quadrupedal and were only facultitatively bipedal because they were herbivorous and, because they did not develop an alternative method for protracting the femur, the pubis had to remain anteroventrally directed and the elongate viscera could not be slung below the pelvis as in ornithopods.

6. Summary

The skeletal material of prosauropod dinosaurs from the Lower Jurassic (Pleinsbachian) of North America is described. Two specimens (AM 41/109, YPM 1883; upper part of Newark Series of Connecticut Valley) are slender-footed, four specimens (YPM 208, 209; Connecticut Valley; MNA G2 7233, UCMP 82961; Navajo Sandstone of Arizona) are broad-footed, and the foot type of YPM 2125 (Connecticut Valley) is indeterminate.

The genus *Anchisaurus* Marsh, 1885 with *Megadactylus polyzelus* Hitchcock, Jr. 1865 (holotype AM 41/109) as the type species is a valid genus. The arguments used to refer *Megadactylus polyzelus* to the genus *Thecodontosaurus* Riley and Stutchbury are shown to be based on misinterpretations of the material. The differences between AM 41/109 and YPM 1883 are considered minimal and are attributed either to differences in preservation or to individual variation. *Anchisaurus colurus* Marsh, 1891 (holotype YPM 1883) is considered a junior synonym of *Anchisaurus polyzelus* (Hitchcock, Jr.) and *Yaleosaurus* Huene, 1932 is a junior synonym for *Anchisaurus* Marsh, 1885.

The family Anchisauridae Marsh, 1885 is restricted to slender-footed taxa, viz. *Anchisaurus polyzelus* (Hitchcock, Jr.), *A. capensis* (Broom), *Efraasia diagnostica* (Huene), and *Thecodontosaurus antiquus* Morris; South African and Australian species of Thecodontosaurus are anchisaurid taxa based on specimens that are generically and specifically indeterminate.

The genus *Ammosaurus* Marsh, 1891 with *Anchisaurus major* Marsh, 1889 (holotype YPM 208) as the type species is a valid taxon. YPM 209 is also broad-footed and cannot be distinguished from YPM 208 by any characters other than a size difference; so *Anchisaurus solus* Marsh, 1892 [*Ammosaurus solus* (Marsh) of Huene (1932)] is considered a junior synonym of *Ammosaurus major* (Marsh). The specimens from Arizona are provisionally referred to as *Ammosaurus* cf. *major*.

An analysis of the characters of *Ammosaurus* shows that this genus is not a primitive coelurosaurian (theropod) dinosaur as commonly throught but a broad-footed prosauropod with three specialized features: a long anterior process to the ilium, a ventral emargination to the subacetabular part of the ischium, and the form of the third sacral rib. These features do not warrant the retention of the family Ammosauridae Huene, 1914a. *Ammosaurus* and the broad-footed taxa previously included within the family Anchisauridae [*Aristosaurus, Lufengosaurus ("Gyposaurus" sinensis, Yunnanosaurus*) and *Massospondylus (Aetonyx, Dromicosaurus, Gryponyx, Leptospondylus, Pachyspondylus*)] are transferred to the family Plateosauridae Marsh, 1895.

Most prosauropods were herbivorous and the food was probably broken down by a gastric mill containing small stones. The replacement of prosauropods by ornithischians as the dominant "small- to medium-sized" (up to 10 m) terrestrial herbivores was probably in part because of the development in ornithischians of a more efficient masticatory apparatus for dealing with resistant plant material, viz. tooth-to-tooth occlusion so teeth were self-sharpening, plus cheeks to prevent the food loss from the sides of the tooth rows during chewing.

Anchisaurids and plateosaurids were basically quadrupedal as shown by the hind limb-to-trunk ratios and the adaptations of the manus to prevent damage to the enormous first ungual of the manus while walking quadrupedally. Sauropodomorphs remained quadrupedal because, in the absence of an alternate mechanism for protracting the femur, the pubis remained anteroventrally directed and the elongate viscera necessary for digesting plant material were not slung more posteriorly below the pelvis as probably was the case in bipedal ornithopod dinosaurs.

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